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A MONOGRAPH OF THE GENUS
HYDRANGEA

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PREFACE

Hydrangea, a woody genus of the Saxifragaceae, has been a popular garden and greenhouse plant since the importation of *Hydrangea macrophylla* into England from China by Sir Joseph Banks in 1789. The genus is of interest to botanists because of its disjunct distribution. It occurs in the temperate regions of eastern Asia and eastern North America and extends southward into the tropics of both hemispheres. A temperate group with a deciduous habit has had its greatest development in eastern Asia, while a tropical group with an evergreen habit has had its greatest development in Central and South America. The plants in cultivation have come chiefly from the deciduous group.

Throughout its wide range in both the Old and New worlds *Hydrangea* is fairly abundant and has been much collected over a period of years. Many species have been described from these collections and also from cultivated plants. This has resulted in a multiplicity of names in the genus. No revision of the genus has been done for many years; therefore, for horticultural, as well as for botanical purposes, it seemed desirable to revise the genus thoroughly, to find out the morphological and geographical limits of the species, and to find out the relationship which exists between the New World and the Old World groups.

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A	Arnold Arboretum of Harvard University, Cambridge, Massachusetts.
BH	Bailey Hortorium of Cornell University, Ithaca, New York.
BM	British Museum of Natural History, London, England.
CAS	California Academy of Sciences, San Francisco, California.
CNC	University of North Carolina, Chapel Hill, North Carolina.
DUKE	Duke University, Durham, North Carolina.
E	The Royal Botanic Garden, Edinburgh, Scotland.
G	Conservatoire et Jardin Botaniques, Geneva, Switzerland.
GA	University of Georgia, Athens, Georgia.
GH	Gray Herbarium of Harvard University, Cambridge, Massachusetts.
K	The Royal Botanic Gardens, Kew, England.
K-W	The Wallich Herbarium of the Royal Botanic Gardens, Kew.
KRA	Universitatis Jagellonicae, Krakow, Poland.
KY	The University of Kentucky, Lexington, Kentucky.
MEDEL	Herbario de la Facultad Nacional de Agronomia, Medellin, Colombia.
MICH	The University of Michigan, Ann Arbor, Michigan.
MO	Missouri Botanical Garden, St. Louis, Missouri.
NY	New York Botanical Garden, New York, New York.
O	Botanisk Museum, Oslo, Norway.
OKL	Bebb Herbarium of the University of Oklahoma, Norman, Oklahoma.
P	Muséum National d'Histoire Naturelle, Laboratoire de Phanérogamie, Paris, France.
S	Naturhistoriska Riksmuseet, Botanical Department, Stockholm, Sweden.
TENN	The University of Tennessee, Knoxville, Tennessee.
TI	Botanical Institute, University of Tokyo, Tokyo, Japan.
UPS	Institute of Systematic Botany, Botanical Garden and Botanical Museum of the University of Uppsala, Uppsala, Sweden.
UC	The University of California, Berkeley, California.
US	National Museum, Smithsonian Institution, Washington, D. C.
W	Naturhistorisches Museum, Vienna, Austria.
WU	Botanisches Institut und Botanischer Garten der Universität Wien, Vienna, Austria.
WVA	West Virginia University, Morgantown, West Virginia.

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INTRODUCTION

The name *Hydrangea* was first used by Gronovius (1739) in his *Flora Virginica* for a plant collected by John Clayton. Linnaeus (1753) adopted this name when he described *Hydrangea arborescens* in the *Species Plantarum*. This, the first species to be described in the genus, was followed by *H. radiata*, which was named by Thomas Walter (1788) in the *Flora Caroliniana*, and *H. quercifolia*, named by William Bartram in 1790 in the account of his travels through the Carolinas, Georgia, and Florida. Ruiz and Pavón made the first collection of a species of the genus in South America, but they referred their plant to the genus *Cornidia* (1798). *Cornidia umbellata* Ruiz & Pavón is now referred to *Hydrangea Preslii* Briquet. The first Asiatic species of the genus were placed in *Viburnum*. In 1781 the younger Linnaeus described one species, and in 1784 Carl Thunberg described five in his *Flora Japonica*.

Because of the ornamental value of some species of *Hydrangea*, many of the early collections of the genus were actually made for the purpose of introducing the plants into gardens. *Hydrangea arborescens*, the first species to be cultivated in England, was said by William Curtis (1799) to have been introduced into England as early as 1736. Philip Miller (1768) stated that it had "been brought within a few years past to Europe, and is now preserved in gardens for the sake of variety more than its beauty." Apparently, this species was never as popular a garden plant as the next hydrangea to be introduced into England, the one we know today as *Hydrangea macrophylla* subsp. *macrophylla*. Through the agency of Sir Joseph Banks a living plant of this hydrangea was brought to the gardens at Kew from China in 1789. It was named *H. hortensis* by Sir James E. Smith (1792). *Hydrangea hortensis*, however, was the same as the plant described by Thunberg in 1784 as *Viburnum macrophyllum*. Thunberg's name was overlooked until Seringe (1830) transferred it from *Viburnum* to *Hydrangea*. The plant, however, was not overlooked. As *Hortensia opuloides* it was described by Lamarek (1790). This name was based on a specimen cultivated at Mauritius and probably sent to France by Commerson. The Portuguese missionary, Loureiro, who spent many years in Indo-China, in 1790 described a plant as *Primula mutabilis* which was apparently a cultivated specimen of *Hydrangea macrophylla* subsp. *macrophylla* (see Merrill, 1935). Other names were given to this plant by Siebold who during the several years which

he spent in Japan collected a number of horticultural forms of hydrangea. Siebold's names were published and described (1829) in a synopsis of the Japanese species of *Hydrangea*. Later (1840) some of these were illustrated in Siebold and Zuccarini's *Flora Japonica*.

During the early part of the nineteenth century other Asiatic species were discovered and named. *Hydrangea anomala*, *H. aspera*, and *H. heteromalla* were found in the eastern Himalayas by Francis Buchanan-Hamilton and Nathaniel Wallich. These same species were collected again by J. D. Hooker and Thomas Thomson during their explorations of the eastern Himalayas in 1848-1850. So far as known no material was introduced into cultivation from these collections.

The first complete taxonomic treatment of the genus was that of Seringe (1830) in DeCandolle's *Prodromus*, which brought together the species from both the Old and New worlds known to that time. In treating the South American species he apparently overlooked the genus *Cornidia* of Ruiz and Pavón, but he did include *Sarcostyles* of Presl, in which was placed *Sarcostyles peruviana* Presl, now referred to *Hydrangea Preslii*. The other South American species which he included were *H. peruviana* Moricand and *H. scandens* Poeppig, now referred to *H. serratifolia*. He included among the Asiatic species not only the Japanese species described by Thunberg (1784) and Siebold (1829) but also *H. oblongifolia* Blume (now placed in synonymy under *H. aspera*) from Java, and the species from the eastern Himalayas described by Wallich (1826) and David Don (1825).

Maximowicz (1867) published an important revision of the eastern Asiatic species known at that time. These species he divided into two sections: Euhdrangea, for those which are erect in habit and have petals which fall separately and possess elliptic seeds, and Calyptranthe for those which are scandent in habit and have petals which are coherent and fall as a cap and possess circular seeds. Euhdrangea he divided into Series 1, Petalanthe, for those in which the petals are persistent and reflexed during anthesis and the seeds are not caudate, and Series 2, Piptopetalae, for those in which the petals are usually deciduous in early anthesis and the seeds are caudate. He divided Petalanthe into two groups, Americanae, for the North American species, and Japonico-sinensis, for *Hydrangea hirta*, *H. virens*, and *H. chinensis*. Koehne, treating only the cultivated species of the groups previously considered by Maximowicz, divided them into two subgenera, *Hortensia* for *H. opuloides*, and *Hortensiella* for the remainder of the species. This latter subgenus he divided into Euhdrangea and Calyptranthe.

Engler's summary of the genus (1891) recognized Euhdrangea and Calyptranthe as originally constituted by Maximowicz, and in addition established a third section, *Cornidia*, for the scandent evergreen species of

Central and South America. Schneider's treatment (1906) of the cultivated species was based essentially on that of Engler, except that he called Engler's sections subgenera. Rehder (1911), treating only the Chinese species, recognized Euhdrangea and Calyptranthe as constituted by Maximowicz. Euhdrangea he divided into three subsections. In Petalanthe he included only those species which Maximowicz had grouped together as Japonico-sinensis. Heteromallae was a new subsection for *H. paniculata* and *H. heteromalla*, and Asperae was new for *H. aspera*. Later (1927), in a treatment of the cultivated species, Rehder added a fourth group under Euhdrangea, Americanae, for the North American species. He refers to these subdivisions as "Groups" in 1927, but in 1940 and 1949 he refers to them as "Series." Engler (1930), in a brief treatment of the genus, recognized Rehder's subdivisions which he called subsections.

Briquet (1919) revised the Central and South American species and followed Engler (1891) by placing them in the section Cornidia. Briquet divided this section into two subsections, Monosegia and Polysegia, based on the structure of their inflorescences.

The present treatment of *Hydrangea* differs from previous ones in two respects. First, only two sections, Euhdrangea, which must be called section Hydrangea according to a new rule adopted at the meeting of the International Botanical Congress held in Paris in 1954 (Stafleu, 1954), and Cornidia are recognized. The section Calyptranthe, established by Maximowicz and recognized by everyone since, is made a subsection under the section Hydrangea. The characters on which Calyptranthe was based do not appear to be of the same importance as those on which the sections Hydrangea and Cornidia are constituted in the present treatment. Second, *Hydrangea macrophylla* (*H. opuloides* and *H. serrata*) is removed from subsection Petalanthe, in which it had been placed by Rehder and later by Engler, and put into a subsection by itself, designated in the present treatment as subsection Macrophyllae.

MORPHOLOGY AND INFRAGENERIC DIVISIONS

The characters used for dividing Hydrangea along sectional lines are the following:

HABIT. Erect or scandent. When scandent the plants cling by means of aerial rootlets.

FOLIAGE. Evergreen or deciduous.

LEAF TEXTURE. Coriaceous or chartaceous.

FLORAL BRACTS. Rounded or lanceolate. *Rounded bracts*, several in number, occur in a row at the base of the inflorescence. These envelop the unopened inflorescence, and leave noticeable scars on falling. *Lanceolate bracts*, usually numerous, occur throughout the inflorescence. These

may cover, but do not envelop the unopened inflorescence and leave no scars on falling.

The characters used to distinguish and delimit the two sections are the following:

HYDRANGEA	CORNIDIA
Habit usually erect.	Habit usually scandent.
Foliage deciduous.	Foliage evergreen.
Leaf texture chartaceous.	Leaf texture coriaceous.
Floral bracts usually lanceolate.	Floral bracts rounded.

The characters found useful in delimiting the species in the present study are relatively clear cut and overlap very little from one species to another. The use by previous workers of extremely variable characters in describing new species, such as leaf pubescence and shape and size of the leaves, has given the genus an unwarranted reputation for being difficult. A discussion of the variation found in the principal morphological characters follows:

LEAVES. In shape the leaves are usually ovate, varying from narrowly so to broadly ovate. Their margins are usually serrate or entire, although in two species they are pinnately lobed. In size, they vary in length from about two to thirty-five centimeters. In certain species shape and size of leaves are relatively constant, while in others both of these are extremely variable.

A dimorphic condition of the leaves, which exists in the climbing species of the section Cornidia, is associated with a sterile, and perhaps juvenile, growth form. In this form the leaves are usually 1.5–3 cm. long, dentate, chartaceous, and are borne on slender, epiphytic thread-like stems. According to Standley (1937), this growth form is very frequent in occurrence in the temperate region of Costa Rica, growing on tree trunks and fence posts. Because the sterile or juvenile leaves are very different from those on the flowering branches, the relationship between the two kinds of leaves was long unrecognized. Specimens with the sterile leaves only have been seen from Panama, Guatemala, El Salvador, Nicaragua, Peru, and Chile. The specimens from El Salvador and Nicaragua are of particular interest because no flowering material has been collected from either of these countries. *Hydrangea anomala*, a climber from eastern Asia and a member of the section Hydrangea, also has sterile or juvenile leaves, as shown by two specimens in the herbarium at Kew, collected by Hooker and Thomson at Darjeeling.

PUBESCENCE. The type of pubescence is usually uniform within each species, but its density may vary. Only in *Hydrangea arborescens* and *H. quercifolia* is there more than one kind of hair. In section Hydrangea the hairs are slender, about 0.3–1 mm. long, and white. Under a magnifi-

cation of 35 or 45 diameters their surfaces appear rough, like frosted glass; under magnification of about 350 diameters their surfaces are seen to be covered with minute tubercules (see plate 3, figure 4). These hairs are sometimes stiff and appressed and at other times soft and curled. In *H. arborescens* subsp. *radiata* the hairs have no tubercules and are smooth. In *H. quercifolia* both the smooth and rough surfaced hairs are combined on the lower leaf surfaces. In section Cornidia the more common kind of hair is short (0.1–0.3 mm. long), stiff, light brown, and borne in stellate clusters. The less common type consists of single, longer hairs (0.4–0.6 mm. long), which are curled, and light brown or ferruginous in color.

INFLORESCENCE. The inflorescence in *Hydrangea* may be described in general terms as a dendritically branched, terminal cluster, usually many-flowered, and either rounded or pyramidal in shape. The rounded cluster is the more common, being found in all but two species, *Hydrangea quercifolia* and *H. paniculata*, which have pyramidal clusters. The dendritic branching of the inflorescence is arranged in such a way that the flowers are held erect and more or less in the same plane.

The ultimate members of the dendritically branched system, of which the rounded clusters are composed, consist of single flowers or small clusters of two to six flowers. These clusters correspond to modifications of a simple dichasium, which, as defined by Rickett (1943, p. 489), consists of a "short branch bearing a terminal flower and two prophylls which subtend as many lateral flowers." Rickett (1943), in discussing the inflorescence of *Crataegus*, interprets the terminal flower groups in the inflorescence of *C. Crus-galli* as being dichasia. In some dichasia the terminal flower opens first, and in others the three flowers open approximately together. However, there are other flower groups with different numbers of flowers. Such groups represent condensations of dichasia, in which one or two flowers have failed to develop and which are aggregated in a rather irregular fashion upon a central axis. The inflorescence of *Hydrangea* is made up of terminal units similar to those of *Crataegus*. These terminal units appear to represent modified dichasia with an irregular number of flowers which appear to open at approximately the same time. The entire inflorescence consists of an aggregation of irregular groups upon a central axis, several of which are joined together on a main rachis to form a rounded compound cluster. For such an inflorescence Rickett has proposed to use the term "cyme," redefining it so that it does not refer to a sequence of flowering of the inflorescence.

The pyramidal cluster found in *Hydrangea quercifolia* and *H. paniculata* has been called a panicle, or occasionally a thyrsoid cyme. Examination of the ultimate units of the inflorescences of these two species shows them to be single flowers or small clusters which appear to be modifications of simple dichasia and not different from those of the species

having the rounded clusters. These ultimate units are aggregated into branches which are scattered upon an elongate central rachis, and the whole inflorescence differs from the cyme, as redefined by Rickett, in its pyramidal form. For this inflorescence the term *thyse* (Rickett, 1944), that is, a compound flower cluster of more or less pyramidal form whose ultimate units are simple dichasia, may be used. In this definition no reference is made to sequence of flowering of the inflorescence. However, in both species of *Hydrangea* having this kind of inflorescence there is a sequence of flowering from the bottom to the top of the inflorescence, the lowermost clusters opening before the uppermost.

The main branches of the inflorescence in the section Cornidia all arise at one point, giving the inflorescence an "umbellate" appearance. The arrangement of these umbel-like cymes is used as a basis for dividing the section into two subsections. The cymes occur singly in the subsection Monosegia, while in the subsection Polysegia there are several which occur one above another along a main axis. In the section *Hydrangea* the main branches do not arise at the same point, although sometimes their points of origin are close enough to present an "umbellate" appearance. The type of *Hydrangea umbellata* Rehder, now considered to belong to *H. scandens* subsp. *chinensis*, has such an inflorescence. In only one instance are a pair of closely related species separated by the differences in their inflorescences. The chief difference between *H. heteromalla* and *H. paniculata* is the rounded, cymose inflorescence of the former and the pyramidal one of the latter.

FERTILE FLOWERS. Variations in floral structure involve in some degree most of the parts of the fertile flowers.

HYPANTHIA. The ovary is fused wholly or in part with the receptacle and this fused portion is here called the hypanthium. When the fusion is complete, the top of the hypanthium, called the disk, is flat. When fusion is incomplete and only the lower part of the ovary is fused to the receptacle, the disk is conical.

SEPALs. The sepals are deltoid, relatively short (usually less than 1 mm. long) and inconspicuous. Their number is the same as that of the petals, that is, either four or five.

PETALS. The petals are always valvate and vary little in size (usually about 2 mm. long). In shape they are somewhat ovate or obovate. When ovate, they are truncate at the base; when obovate, they are narrowed at the base (see plate 6, figures 2B and 4B). In one species the petals cohere and fall as a cap or calyptra (see plate 5, figure 4B).

STAMENS. The stamens are usually 8 or 10, that is, twice as many as the sepals or the petals. In only one taxon (*Hydrangea anomala* subsp.

petiolaris) is their number three or four times that of the sepals or the petals.

PISTILS. Variation in the pistil is found in the number of its parts and in its relation to the hypanthium. The number of locules in the ovary and the number of styles vary from two to five, often with variation in the same species or even on the same plants. The relation of the ovary to the hypanthium has already been mentioned. The position of the ovary is a useful character for delimiting subsections and species in the section *Hydrangea*. In the section *Cornidia* the ovary is always inferior. Placentation is always axile. In the inferior ovary the placentas are attached to the central axis which is at the same level as the attachment of the sepals to the hypanthium, while in the half superior ovary the central axis extends upward and under the conical disk. In the half superior ovary the styles arise from the top of the conical disk and their length in comparison with the height of the disk is used as a subsectional character in two instances. The styles, normally separate, show a tendency to adhere during early anthesis in two species of the section *Cornidia*, *Hydrangea diplostemona* and *H. tarapotensis*, becoming separate by late anthesis (see plate 4, figures 7 and 8). The stigmatic surfaces develop from the apex of the styles downward along the inside surface in the form of noticeable papillae. The stigmatic surface may be present and receptive to pollen when the flower opens and the pollen is shed. However, from herbarium specimens it is not possible always to be certain when the stigmatic surface is receptive. In the two North American species the styles appear turgid when the flowers first open and the stigmatic surface is confined to a line extending from the top to a short distance down on the inside surface of the style. Later the stigmatic surface increases and the styles become less turgid. These two species which constitute the subsection *Americanae* are most closely related to the Asiatic subsection *Piptopetalae* on the basis of their both having an inferior ovary. In the subsection *Piptopetalae* the styles from the beginning of anthesis appear slender and have a fairly well developed stigmatic surface. It would thus appear that in the individual flowers of the subsection *Americanae* the stigmas are not receptive to pollen until after the pollen has been shed, while in the flowers of subsection *Piptopetalae* the stigmas are receptive at the same time that the pollen is shed. Observations on living material are necessary to confirm this. In section *Cornidia* there are several species in which it is assumed that the stigmatic surfaces do not develop until after the pollen has been shed. In *Hydrangea Oerstedii* and *H. serratifolia* the styles remain smooth and do not elongate until some time after the flowers are open, and in *H. diplostemona* and *H. tarapotensis* the styles are adherent during early anthesis and the stigmatic surfaces are not exposed at this time.

CAPSULES. The capsules in all species open at the apex between the styles. The shape of the capsules depends on the position of the ovary. When the ovary is inferior, the capsule is truncate at the apex, and when the ovary is half superior, the capsule is conical.

SEEDS. The seeds are numerous, elliptical to oval, and very small (about 1 mm. long). In some species the seeds are caudate, by virtue of the seed coat being attenuate into a short tail-like extension at each end of the seed (see plate 5, figures 1c and 2c). In one species (*Hydrangea anomala*, see plate 5, figure 4D), the body of the seed is surrounded by a circular wing. The mature seeds in all species are variously striate or reticulate.

STERILE FLOWERS. Sterile flowers, formed by the enlargement of the sepals into petal-like structures, are larger and more conspicuous than the fertile ones and occur around the periphery of the inflorescences. In most species, sterile flowers are present in addition to the fertile ones; however, occasionally (as in *Hydrangea arborescens*), they may be present in some individual plants and absent in others. In a few species only fertile flowers are present.

The occurrence of inflorescences consisting entirely of sterile sepaloid flowers led to the early cultivation of *Hydrangea macrophylla* as an ornamental plant. There are similar forms, also in cultivation, of *H. arborescens* and *H. paniculata*. These inflorescences probably originated from a mutation in wild populations and the plants on which they occurred were brought into cultivation. I have seen no collections from the wild of either *H. macrophylla* or *H. paniculata* with this type of inflorescence; however, collections of such have been made in the eastern United States for *H. arborescens*. In *H. aspera*, as judged from a number of herbarium specimens, this condition occurs in the wild. The condition also occurs in *H. Oerstedii*, as has been observed in a single specimen (Linden 1139). The development of sterile sepaloid flowers has taken place in *Cardiandra*, *Platycrater*, and *Schizophragma*, genera which are considered to be related to *Hydrangea*. Superficially, the enlargement of the sepals in some species of *Hydrangea* gives these plants a resemblance to certain species of the unrelated genus, *Viburnum*. In *Viburnum*, however, it is the petals of the showy flowers which have become enlarged and sterile.

The presence of sterile flowers has given rise to various speculations as to their function. Kerner von Marilaun (1902) suggested that in *Hydrangea quercifolia* they are a means of protecting the pollen of the fertile flowers from rain. Their role in attracting insects to the inflorescence has been considered. Plateau (1898) did not consider this to be of prime importance but felt that pollination of the fertile flowers would be accomplished regardless of the presence or absence of the sterile ones

because, first, in the case of the inflorescences having only a few sterile flowers the insects proceed directly to the fertile flowers, and second, inflorescences having mostly sterile flowers are seldom visited by insects.

The peripheral sterile flowers ordinarily consist of only the enlarged calyx. However, in some of the garden forms of *Hydrangea macrophylla* in which the inflorescences consist almost entirely of sterile flowers, petals, stamens, and pistils may be present also. Such flowers are not sterile although they probably do not often set seed. Perriraz (1911) reported unsuccessful attempts to obtain seeds from such flowers. He further reported that plants of the garden form known as *H. macrophylla Otaksa* having inflorescences composed of enlarged showy flowers, changed the composition of their inflorescences over a period of years so that fewer showy flowers and more fertile ones are produced.

The floral structure in *Hydrangea* is essentially the same throughout the genus. The two sections are separated on the basis of vegetative characters and habit; not a single floral structure can be found to separate them. The half superior ovary present in some species of *Hydrangea* may be considered more primitive than the inferior ovary. However, the development of the inferior ovary is not associated with a single other advanced structure in those species in which it occurs. In addition to the inferior ovary present in some species, the reduced number of stamens (which are double the number of the petals) is also an advanced character. The separate actinomorphic petals, numerous seeds, and the large spreading cymose inflorescences with numerous small flowers are primitive. This combination of characters, together with the uniform floral pattern throughout the genus, becomes somewhat more significant when considered in relation to the method of pollination in *Hydrangea*.

The Saxifragaceae as a family is placed by Grant (1949) in a group, designated as "Promiscuous Plants," pollinated by miscellaneous insects. Grant made a survey of the taxonomic characters used to distinguish species in various families of angiosperms and he found a correlation between the importance of floral structures used in classification and method of pollination. Species pollinated by miscellaneous insects are less frequently found to have differences and trends in floral structures than are those pollinated by specific insects. The only observations available regarding pollination in *Hydrangea* are those made by Robertson (1892) on *H. arborescens*. These showed that certain unspecialized members of the Hymenoptera, Diptera, Coleoptera, and Lepidoptera visited this species. Although similar observations are not available for other species in the genus, it may be assumed that since the floral structure and the characters of the inflorescence in *H. arborescens* follow the pattern for that of the genus, the same type of insect visitors would be present on other species.

The presence of the sterile peripheral flowers and numerous small flowers arranged in cymose inflorescences gives *Hydrangea* a superficial resemblance to certain species of *Viburnum* (Caprifoliaceae). In *Viburnum*, however, there are several advanced characters not present in *Hydrangea*: the corolla is united, the stamens are reduced to the same number as the parts of the corolla, and the ovules are reduced to one in each carpel. The presence of these characters places *Viburnum* in a family considered unrelated to the Saxifragaceae and shows a beginning in the direction of specialization in both floral structure and methods of pollination found in the more highly developed genera of the family. Robertson's (1898) observations on insect visitors to *Viburnum pubescens* Pursh and *V. prunifolium* L. showed much the same aggregation of miscellaneous insects as he had observed on *Hydrangea arborescens*. Therefore, in spite of the presence of the several advanced characters just mentioned for *Viburnum*, this genus would be classed with the group of Promiscuous Plants to which *Hydrangea* and other saxifragaceous plants belong. Another group of plants which have numerous small flowers aggregated into a dense inflorescence is the Umbelliferae which has an inferior ovary and reduced number of stamens and seeds, but (as *Hydrangea*) separate actinomorphic petals. Undoubtedly, dense inflorescences made up of numerous small flowers serve as a landing place for various unspecialized insects which effect pollination through their movements. This is a device found to be successful in several unrelated families of angiosperms and one not associated with diversified or specialized floral structures.

Natural hybrids in *Hydrangea* are rare. The only report known to the writer of the occurrence of such a hybrid is that made by Makino (1932). He described a plant, growing on Izu Peninsula, Honshu Island, Japan, which he considered to represent a hybrid between *H. hirta* and *H. scandens*. These two very closely related species differ chiefly in the shape and margin of their leaves. An illustration of the reputed hybrid showed leaves more or less intermediate between the two putative parent species (Hiyama, 1934).

Hybrids have been reported in cultivation but crosses must be difficult to effect since the reports have been few. Haworth-Booth (1950) lists the following:

1. A hybrid between *Hydrangea macrophylla* var. *rosea* and *H. paniculata*, reported by Monsieur L. Foucard, horticulturist in Orleans, France, in 1912. The plant was pictured in *Revue Horticole* (1912, p. 324) and showed corymbose (not paniculate) inflorescences consisting entirely of sterile flowers.

2. A hybrid between *Hydrangea macrophylla* var. *rosea* and *H. petiolaris*, called *H. × hortentio-laris*, was made by Monsieur Henri Cayeux of Le Havre, France.

According to Haworth-Booth, both of these plants were lost before they became established in the horticultural trade.

Sax (1931) reported chromosome counts for several species in the section *Hydrangea*. *Hydrangea arborescens*, *H. radiata*, *H. cinerea*, *H. petiolaris*, *H. paniculata*, and *H. ranthoneura* all had a diploid number of 36, with the exception of 72 in a horticultural form of *H. paniculata*. Sugiura (1931) reported a haploid count of 18 for *H. virens*, and Haworth-Booth (1950) reported counts made of various garden forms of *H. macrophylla* by Dr. Janaki Ammal which also showed a diploid count of 36. So far as known, no counts have been made of species in the section *Cornidia*.

GEOGRAPHIC DISTRIBUTION

The occurrence of *Hydrangea* in eastern Asia and eastern North America places it in that group of genera which indicate a relationship between the floras of these two regions. The problem of this disjunct distribution has recently been discussed and reviewed by Li (1952). Li lists two groups of genera which are especially confined to eastern Asia and eastern North America, those which are distributed in temperate regions in both areas, and those distributed in the temperate regions and also in the tropical (or subtropical) regions in one or both areas. *Hydrangea* falls into the latter group, since both in Asia and America there are species found in temperate and subtropical regions. Map 1 shows the distribution of the genus.

The section *Hydrangea* occurs in the temperate regions of eastern Asia and eastern North America. Its greatest development is in eastern Asia where nine of its eleven species are found. In this area it extends from the Himalayas eastward across central and southern China to Sakhalin, Japan, the Ryukyu Islands, the Philippine Islands, Formosa, Sumatra, and Java. The center of this large area (with reference to *Hydrangea*) is western and central China, where six of the nine species occur. This region includes Kweichow, Yunnan, Szechuan, and parts of Kwangsi, Hunan, and Hupeh, and within it are the Yangtze Valley and the high mountains of southwestern China. The vegetation characteristic of the middle elevations of this region is a deciduous mesophytic forest known to be the richest of all present day temperate floras. The richness of this flora may be attributed to the topography and mild climatic conditions of the region and also to the lack of extensive Pleistocene glaciation. The occurrence of *Hydrangea* within this area follows the distributional pattern of many of the genera which are disjunct between eastern Asia and eastern North America.

Li (1952) pointed out that in eastern Asia the distribution of species in these disjunct genera is often widespread. Such genera occur in the same regions where the widespread species of *Hydrangea* are found. The

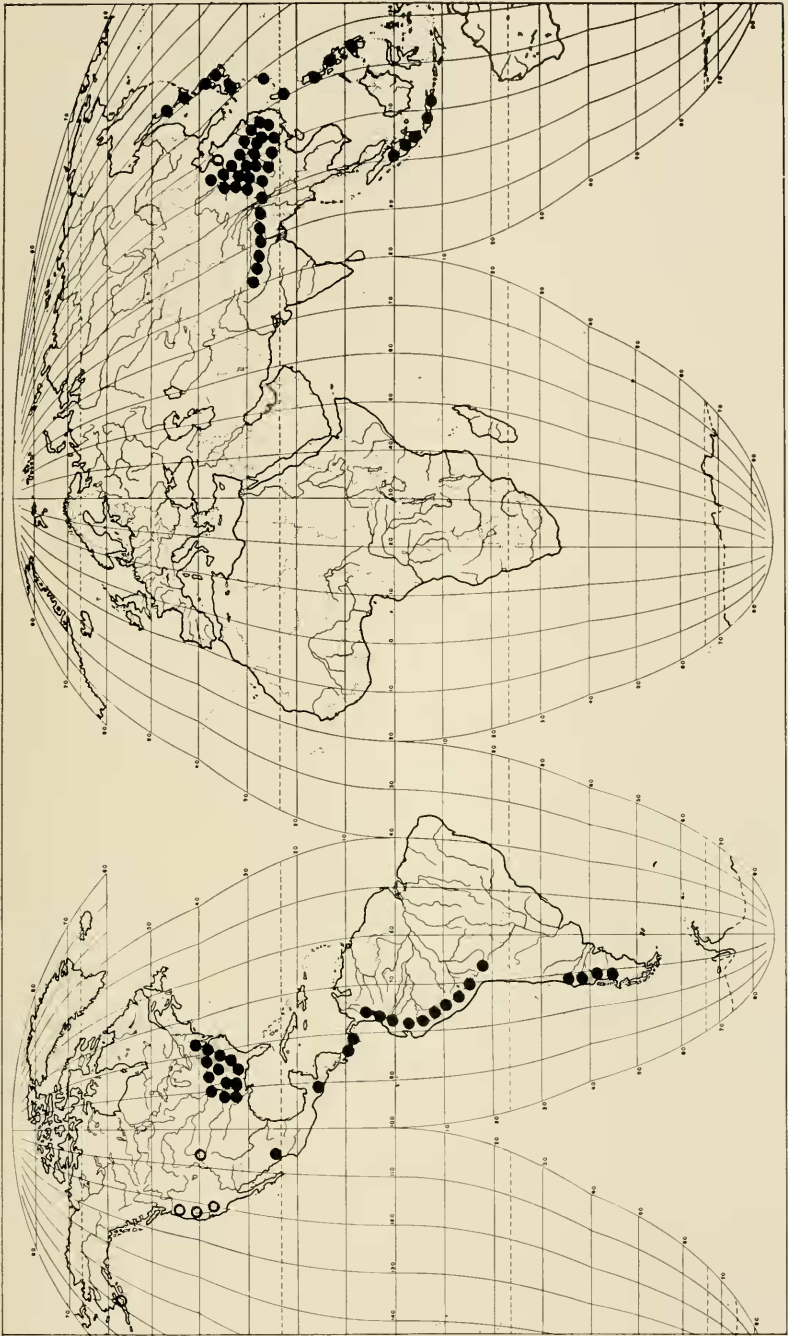
extension of some genera into the warmer subtropical areas such as the mountains of the Philippines, Sumatra, and Java is not uncommon, but these islands may be considered to represent peripheral areas in the distribution of these genera. In discussing the relationship between the floras of Formosa and southwestern and central China, Wilson (1920) stated that the climate of Formosa is warm temperate, but that in the mountains such cool temperate genera as *Fagus*, *Ulmus*, *Carpinus*, *Alnus*, and *Malus* reach their southern limits. Merrill (1934) pointed out that certain southern Asiatic species make a jump to the higher altitudes of Sumatra, Java, Borneo, and the Philippines but do not occur in the Malay Peninsula.

Hydrangea, as many genera of the eastern Asiatic-eastern North American relationship is found in Japan. Some species of *Hydrangea* found in Japan are widespread in China, while others are confined to Japan or to Japan and such adjacent areas as Formosa, Korea, and the Ryukyu Islands. The relationship of the flora of Japan to that of central and western China has been discussed by Hu (1940) who attributes this relationship in part to the fact that Japan was connected to the Asiatic mainland up to the middle of the Tertiary period.

The two species of *Hydrangea* found in North America occur in the deciduous mesophytic forest of the eastern United States. Both appear to be centered in the southern Appalachian Mountains. The Appalachian area, being an upland plateau and not glaciated, is known to have been continuously available for plant life since long before the beginning of the Tertiary period. It represents an area of refuge for the eastern Asiatic-eastern North American disjunct genera which were more widespread during the Tertiary period than they are now. Cain (1943) has pointed out the Tertiary affinity of many of the genera of the cove hardwood forests of the southern Appalachians.

In contrast to the temperate occurrence of the species belonging to the section *Hydrangea*, those of the section *Cornidia* are found in the subtropical regions of Central and South America, where twelve species extend from Guatemala through Costa Rica and Panama and into the Andes of South America. A single restricted species occurs in the Sierra Madre in Durango, Mexico. All of the species of *Cornidia* in this region occur in the mountainous areas where temperatures are moderate and where there are mists or frequent rains. This subtropical element of *Hydrangea* differs from the temperate element in its thick coriaceous evergreen leaves and generally climbing habit. The species of *Cornidia* are not confined to the New World; a single species, *Hydrangea integrifolia*, occurs in the mountains of the Philippines and Formosa.

The present day disjunct distribution of the temperate mesophytic forests of eastern Asia and eastern North America can be better under-



MAP 1. Distribution of living and fossil species of *Hydrangea*. ● Living species. ○ Fossil species.

stood by a knowledge of the past distribution of a similar forest which was composed of many of the same woody genera. Fossil records indicate that a deciduous mesophytic forest extending as far north as Manchuria, Greenland, and Alaska existed during the early and middle parts of the Tertiary period over a considerable portion of the northern hemisphere. This forest belongs to the so-called Arcto-Tertiary flora.

The northwestern part of North America has provided a fairly complete chronological record of the history of the Arcto-Tertiary flora in this region. The changes in the composition of this flora have been outlined by Chaney (1940) on the basis of a series of fossil floras. The various fossil floras from Eocene through Miocene times in western North America show that there were for any period of time latitudinal and altitudinal variations in composition of the vegetation, but that as the climate changed from warm and wet in the earlier part of the Tertiary to cool and dry in the later part, the vegetation changed also. The climatic trend toward lower temperature and precipitation resulted in the elimination of an evergreen neotropical flora, which existed as far north as Oregon, by the end of the Oligocene, and in the southward migration of a temperate deciduous flora of higher northern latitudes to replace it. By early Miocene times the redwood and broad-leaved, deciduous trees were dominant in Oregon. The Bridge Creek flora of the John Day Basin, late Oligocene or early Miocene, contains (Chaney, 1944) redwoods and broad-leaved deciduous trees characteristic of a wet summer climate. Other Miocene floras of the same age were of similar composition. However, during the Miocene, the Cascades were uplifted and with the changes in topography and climate, the redwoods and broad-leaved trees began to disappear. The Mascall flora of later Miocene showed that trees such as black and live oaks, box elders, madroño, sycamores, and poplars began to replace the trees requiring more moisture. By the Pliocene, redwoods and other moisture requiring trees had nearly disappeared. *Hydrangea*, which belonged to this mesophytic element, is not reported after the Miocene in western North America.

LaMotte (1952) lists six fossil species of *Hydrangea* from Eocene, Oligocene, and Miocene deposits in southern Alaska, Washington, Oregon, California, Idaho, and Colorado. These species and their places of collection are as follows:

- H. alaskana* Hollick. Paleocene or Eocene. Jaw Mountain, Alaska Peninsula, Alaska.
- H. californica* MacGinitie. Eocene. Ione Gravels: Chalk Bluffs, Nevada County, California.
- H. russellii* Chaney & Sanborn. Eocene-Oligocene. Fisher: Goshen, Lane County, Oregon.
- H. fraxinifolia* (Lesquereux) Brown. Oligocene. Florissant, Colorado.

H. reticulata MacGinitie. Oligocene. Weaverville, Hay Fork, Trinity County, California.

H. bendirei (Ward) Knowlton. Miocene. Mascall: Grant County, Oregon. Latah: Spokane, Washington. Whitebird, Idaho. Trout Creek, Harney County, Oregon.

Hydrangea is thus seen to be a member of several fossil floras in western North America from early to middle Tertiary (see Map 1). Its typical occurrence was in the temperate mesophytic forest characteristic of the Arcto-Tertiary flora; however, it is known also from one of the warm humid neotropical floras present in the Pacific Northwest during early Tertiary times. Its presence in the Goshen flora indicates that the subtropical element of the genus, occurring now in Central and South America, may have had a northward extension in the Pacific Northwest. As this neotropical flora died out and was replaced by temperate floras, the subtropical element of *Hydrangea* was also lost in the area.

These records of *Hydrangea* in the Tertiary floras of the west constitute the only fossil records of this genus in North America. In eastern North America, Tertiary fossil plants are known only from the southeastern Gulf Coast. Although *Hydrangea* occurs today in the eastern United States, it is not found in any of these deposits.

In China, *Hydrangea* is reported from the Miocene Shanwang flora in Shantung Province by Hu and Chaney (1940), who show that the majority of Shanwang genera are wide ranging in China today and that this fossil flora includes elements which now characterize the forests of central and south China and the Yangtze Valley. Many of these are temperate northern genera, and although they are found today in middle and upper levels in the mountains, they are rare or absent from lower altitudes in these areas. The Shanwang flora is the only record of Miocene vegetation in China. As in western North America, *Hydrangea* is not found in China in deposits later than the Miocene. Pliocene floras of the northern interior of China lack the mesophytic elements present in the Shanwang flora. Hu and Chaney also showed that the modern forests of Korea and Japan were very similar to the Miocene vegetation of northern China, but that Pliocene floras from Japan are not different from central Japanese forests of today.

THE SPECIES IN CULTIVATION

Hydrangeas were cultivated in China and Japan long before their introduction into Europe and America, and many of our garden forms came from the Orient. There is no way of knowing how long these forms had been grown by the Chinese and Japanese; we merely know that many Europeans, including Thunberg, Siebold, Fortune, and Maximowicz, found

these plants as well established horticultural subjects in China and Japan before they sent them to Europe. As with other horticultural plants having forms which are the result of many generations of selection, their origin is lost in obscurity. A discussion of the origin of the cultivated forms of *Hydrangea macrophylla* is given under that species. Haworth-Booth (1950) has discussed the horticultural aspects of the genus in his recent book, *The Hydrangeas*. Since Haworth-Booth has covered the subject adequately, the present discussion of *Hydrangea* as a garden plant will only list the species cultivated, together with some of the synonyms by which they are often known. Complete synonymy is given under each of the species mentioned.

1. *Hydrangea macrophylla*. Of the species listed, this one has always been the most popular because of its versatility, both as a garden plant and as a florists' plant. *Hydrangea macrophylla* subsp. *macrophylla* var. *macrophylla* (*H. Hortensia*, *H. hortensis*, *H. opuloides*, *Hortensia opuloides*). This is the form to which belong the many globose-headed plants with all sterile flowers called hortensias. *Hydrangea macrophylla* subsp. *macrophylla* var. *normalis* is the form to which belong the plants with a few sterile flowers surrounding a cluster of fertile flowers. Haworth-Booth calls these lacecaps. *Hydrangea macrophylla* subsp. *serrata* (*H. serrata*) is said to be in cultivation, but it is so similar to subsp. *macrophylla* that it is very difficult to recognize garden forms as actually belonging to this subspecies.

2. *Hydrangea arborescens* subsp. *arborescens*. A form of this subspecies with all sterile flowers, called *H. arborescens grandiflora*, is often cultivated. Subsp. *discolor* (*H. cinerea*) and *radiata* (*H. radiata*) are occasionally cultivated.

3. *Hydrangea quercifolia*.

4. *Hydrangea paniculata*. A form of this species with all sterile flowers, known as *H. paniculata grandiflora*, is called the "peegee" hydrangea.

5. *Hydrangea heteromalla* (*H. xanthoneura*, *H. Bretschneideri*, *H. vestita*).

6. *Hydrangea anomala* subsp. *petiolaris* (*H. petiolaris*, *H. scandens*). This plant is often erroneously called *Schizophragma hydrangeoides*, a quite different Asiatic climber.

7. *Hydrangea involucrata*. A form of this species with inflorescences consisting of all sterile flowers has been cultivated in Japan. It apparently has not been introduced into the United States.

8. *Hydrangea aspera* subsp. *aspera* (*H. villosa*). *H. aspera* subsp. *strigosa* (*H. strigosa*, *H. aspera* var. *macrophylla*). *H. aspera* subsp. *robusta* (*H. longipes*). *H. aspera* subsp. *Sargentiana* (*H. Sargentiana*).

9. *Hydrangea serratifolia* (*H. integerrima*). The only species of the section *Cornidia* to be cultivated.

SYSTEMATIC TREATMENT

Hydrangea Linnaeus, Genera Plantarum 189. 1754.

Hortensia Commerson ex Jussieu, Genera Plantarum, 214. 1789.

Cornidia Ruiz & Pavón, Florae Peruvianae et Chilensis Prodrum, 53, t. 35. 1794.

Sarcostyles Presl ex Seringe in DeCandolle, Prodrum, 4:15. 1830.

Much branched shrubs, erect, or scandent and clinging by means of aerial rootlets; deciduous or evergreen; inflorescences, young branchlets, and leaves variously pubescent; leaves opposite, simple, chartaceous or leathery, penninerved, margins entire, denticulate, or serrate, rarely pinately lobed; inflorescences usually terminal, occasionally axillary, on current year's wood, consisting of compound, much branched clusters, rounded or pyramidal in shape, made up of complicated, dendritically branched systems, the ultimate members of which bear a single flower or small clusters of two to seven flowers; flowers fertile or sterile; fertile flowers small, perfect, usually very numerous, comprising the main body of the inflorescence; calyx tubes adnate to ovary, forming the hypanthium, apices flat or conical; sepals 4 or 5, inconspicuous, deltoid; petals 4 or 5, ovate or spatulate, valvate, deciduous during anthesis, falling separately or rarely together as a cap; stamens 8 or 10, rarely as many as 20, filaments usually as long as petals or longer, filiform, anthers oblong to somewhat rounded; ovary inferior or half superior, 2 to 4, rarely 5 locular, styles 2 to 4, rarely 5, separate when ovary is inferior, united at their bases on top of conical apical disk of the hypanthium when ovary is half superior, stigmas terminal to more or less decurrent on inner surface of styles; ovules numerous, borne on axile placentas; capsules hemispherical or turbinate, dehiscent at apex between the styles; seeds numerous, small, linear or elliptic, sometimes caudate, rarely circular with a wing surrounding body of seed; sterile flowers consisting of 3 to 5 enlarged petaloid sepals, usually lacking other flower parts, conspicuous, few in number, arranged on the periphery of the inflorescences, or in some cultivated forms numerous and comprising the entire inflorescence.

The generic name, *Hydrangea*, is derived from two Greek roots, *hydor*, meaning water, and *angeion*, diminutive of *angos*, meaning vessel or container, in allusion to the shape of the mature capsules.

GEOGRAPHICAL DISTRIBUTION: eastern Asia, from the Himalayas eastward to central and southern China, Sakhalin, Japan, the Ryukyu Islands, Formosa, the Philippine Islands, Sumatra, and Java; eastern North America; mountains of Central America southward into the Andes of South America.

TYPE SPECIES: *Hydrangea arborescens* Linnaeus.

KEY TO THE SECTIONS, SUBSECTIONS, AND SPECIES

- 1a. Plants deciduous, erect or scandent, unopened inflorescence not enveloped by broadly ovate floral bracts (except in *H. involucrata*).
 - Section Hydrangea
 - 2a. Ovary inferior in both anthesis and fruit, capsules truncate at apex, styles separate to their bases.
 - 3a. Seeds with rounded wing surrounding body of seed, petals falling together as a cap or calyptra; plants scandent, clinging by means of aerial rootlets.
 - Subsection Calyptranthe
 6. *H. anomala*
 - 3b. Seeds without rounded wing, petals falling separately, plants erect.
 - 4a. Seeds caudate. (Plants of China and Japan.)
 - Subsection Asperae
 - 5a. Leaves pinnately lobed.
 3. *H. sikokiana*
 - 5b. Leaves not lobed.
 - 6a. Bracts broadly ovate to rounded, few, enveloping the unopened inflorescence, leaving noticeable scars on falling; capsules pubescent.
 4. *H. involucrata*
 - 6b. Bracts lanceolate, numerous, scattered through the inflorescence, covering but not enveloping the unopened inflorescence; capsules glabrous.
 5. *H. aspera*
 - 4b. Seeds not caudate. (Plants of the southeastern United States.)
 - Subsection Americanae
 - 7a. Inflorescence a flat-topped cluster; leaves not lobed.
 1. *H. arborescens*
 - 7b. Inflorescence a pyramidal cluster; leaves pinnately lobed.
 2. *H. quercifolia*
 - 2b. Ovary half superior in both anthesis and fruit; capsules conical at their apices.
 - 8a. Seeds caudate; petals truncate at their bases; styles in fruit shorter than conical disk of capsule.
 - Subsection Heteromallae
 - 9a. Inflorescence a pyramidal cluster, calyx lobes 0.5–1 mm. long.
 9. *H. paniculata*
 - 9b. Inflorescence a flat-topped cluster, calyx lobes 0.8–3 mm. long.
 10. *H. heteromalla*
 - 8b. Seeds not caudate; styles in fruit longer than conical disk of capsule; petals clawed at their bases.
 - Subsection Petalanthe
 - 10a. Inflorescences consisting entirely of fertile flowers, stamens 2 to 3 times as long as styles, leaves with serrations 3–8 mm. deep.
 7. *H. hirta*
 - 10b. Inflorescences consisting of both fertile and sterile flowers; stamens same length as styles to as much as two times their length, leaves entire or with serrations less than 3 mm. deep.
 8. *H. scandens*
 - 2c. Ovary inferior in anthesis, becoming half superior in fruit; capsules conical at their apices.
 - Subsection Macrophyllae
 11. *H. macrophylla*
 - 1b. Plants evergreen, shrubs or lianes clinging by aerial rootlets; leaves leathery; floral bracts broadly ovate, few, enveloping the unopened inflorescence, leaving

noticeable scars on falling. (Plants of Mexico, Central and South America, and one species in the Philippine Islands and Formosa.) Section Cornidia

- 11a. Inflorescence consisting of a single, terminal, flat-topped or rounded cluster; flowers pink or white; sterile flowers present or absent.

Subsection Monosegia

- 12a. Calyx lobes and petals 4 or 5.

- 13a. Leaves oval, broadest near middle; sterile flowers present; calyx lobes broadly deltoid, less than 0.5 mm. long.

- 14a. Branchlets of inflorescence glabrous. (Plants of the Sierra Madre Occidental in the state of Durango, Mexico.)

12. *H. Seemannii*

- 14b. Branchlets of inflorescence pubescent with stellate hairs borne on short epidermal papillae. (Plants of Philippine Islands and Formosa.)

14. *H. integrifolia*

- 13b. Leaves obovate, broadest above middle; sterile flowers not present; calyx lobes deltoid to semi-orbicular, 1-2 mm. long. (Plants of Guatemala.)

19. *H. Steyermarkii*

- 12b. Calyx lobes and petals 4. (Plants of Central and South America, from Costa Rica southward into the Andes.)

- 15a. Flowers white; leaves generally 5-14 cm. long, 3-5.5 cm. wide; branchlets and inflorescence and lower leaf surface ferruginous tomentose with stellate hairs, which may be partly deciduous with age.

13. *H. asterolasia*

- 15b. Flowers pink; leaves generally 10-25 cm. long, 4-15 cm. wide; branchlets and inflorescence pubescent with single or stellate hairs, hairs 0.1-0.5 mm. long.

- 16a. Styles usually 3; sterile flowers absent. 18. *H. Preslii*

- 16b. Styles usually 2; sterile flowers usually present.

- 17a. Styles during anthesis 0.3-1 mm. long and without evident stigmatic papillae; stamens 2-4.5 mm. long.

15. *H. Oerstedii*

- 17b. Styles during anthesis 1-2 mm. long and with evident stigmatic papillae; stamens 0.4-3 mm. long.

- 18a. Stamens 0.4-1.6 mm. long, shorter than or rarely as long as styles; styles always separate.

16. *H. peruviana*

- 18b. Stamens 1.5-3 mm. long, longer than styles; styles usually coherent in bud and early anthesis, separating later.

17. *H. diplostemonia*

- 11b. Inflorescences consisting of a series of rounded clusters, one above another; flowers white; sterile flowers always absent. (Plants of the Andes of South America.)

Subsection Polysegia

- 19a. Styles coherent in bud and occasionally during anthesis.

21. *H. tarapotensis*

- 19b. Styles always separate.

- 20a. Stamens 1-1.5 mm. long, not more than one and one-half times as long as styles. 22. *H. Jelskii*

- 20b. Stamens 3-7 mm. long, three to six times as long as styles.

- 21a. Inflorescence and lower leaf surface densely ferruginous pubescent with stellate hairs. (Plants of northern Peru.)

23. *H. Mathewsii*

- 21b. Inflorescence and lower leaf surface glabrous or lightly pubescent with stellate or simple hairs. (Plants of central Chile and adjacent Argentina.) 20. *H. serratifolia*

Section I. HYDRANGEA

Hydrangea, sect. *Euhydrangea* Maximowicz, Mémoires, Académie impériale des Sciences de St. Pétersbourg, ser. 7, 10(16):6 (Revisio Hydrangearum Asiae Orientalis), 1867.

Hydrangea, subgen. *Hortensiella* Koehne, Deutsche Dendrologie, 187, 1893. In part.

Hydrangea, subgen. *Euhydrangea* (Maximowicz) Schneider, Handbuch der Laubholzkunde, 1:384, 1905.

Deciduous shrubs, usually erect, rarely scandent and clinging by aerial rootlets; leaves membranaceous or chartaceous; bracts lanceolate, scattered throughout inflorescence (except in *Hydrangea involucrata*), bracts occasionally absent; stamens usually 10; ovary inferior or half superior; capsule truncate or conical at apex; seeds elliptic to oval, sometimes caudate.

TYPE SPECIES: *Hydrangea arborescens* Linnaeus.

The repetition of the generic name for the section containing the type species is in accordance with a rule adopted by the Nomenclature Section of the International Botanical Congress held in Paris in 1954 (Stafleu, 1954).

Subsection 1. AMERICANAE

Hydrangea, sect. *Euhydrangea*, subsect. *Americanae* (Maximowicz) Engler, in Engler & Prantl, Natürlichen Pflanzenfamilien, 3, 2a:204, 1930. As Group, Rehder, Manual Cultivated Trees and Shrubs, p. 291, 1927; as Series, Rehder, Manual Cultivated Trees and Shrubs, ed. 2, p. 286, 1940.

Hydrangea, sect. 1, *Euhydrangea*, ser. 1. *Petalanthe, Americanae* Maximowicz, Mémoires Académie impériale des Sciences de St. Pétersbourg, ser. 7, 10(16): 6 (Revisio Hydrangearum Asiae Orientalis), 1867.

Flowers white; ovary inferior; capsules truncate at apex; seeds not caudate. North American species.

TYPE SPECIES: *Hydrangea arborescens* Linnaeus.

1. ***Hydrangea arborescens*** Linnaeus, Species Plantarum, 937. 1753.

Much-branched shrub, 1 to 3 m. tall; deciduous; young branchlets and inflorescence strigose pubescent, or puberulent; leaves ovate, elliptic-ovate, or broadly ovate, acute or acuminate at apex, rounded, subcordate, or cuneate at base, broadest near center or toward base, margins serrate, 6–16 cm. long, 2.5–12 cm. wide, their length usually 1.5 to 2.5 times their width, lower surface glabrous or nearly so, or pilose or tomentose, upper surface glabrous, or with occasional scattered hairs; inflorescence a rounded, compound, much-branched cluster, 5–10 cm. wide; fertile flowers white, very numerous; hypanthium 0.8–1 mm. long; calyx lobes 5, deltoid,

0.5 mm. long; petals 5, oblong, 2 mm. long, falling separately; stamens 10, 1.5–4 mm. long, the 5 longer ones about twice as long as the shorter ones; ovary inferior; styles 2, or rarely 3, 1 mm. long; capsule 2–2.5 mm. long, 2–3 mm. wide at apex, somewhat conical at apex, styles 1.2–1.5 mm. long, ribs of capsule 8 or 9, conspicuous; seeds elliptical, blunt at ends, 0.5–0.8 mm. long, 0.4–0.6 mm. wide, prominently striate; sterile flowers white, sometimes absent, usually 4-lobed, occasionally 3-lobed, lobes ovate or orbicular, 8–15 mm. in diameter. (See plate 4, figure 1.)

DISTRIBUTION: Eastern United States from southern New York southward to the southern Appalachian Mountains, westward to the Ozarkian Plateaus. (See map 2.)

KEY TO THE SUBSPECIES OF *HYDRANGEA ARBORESCENS*

1. Lower leaf surface green, glabrous or nearly so, with hairs, when present, only along the midrib and secondary veins; sterile flowers usually not present.
a. subsp. *arborescens*
1. Lower leaf surface white or gray, variously pubescent; sterile flowers present or absent.
2. Lower leaf surface gray, velutinous, pilose, or tomentose, hairs usually not dense enough to be matted; hairs when examined under magnification of about 50 diameters are seen to be conspicuously roughened by numerous tubercles.
b. subsp. *discolor*
2. Lower leaf surface usually white or silvery, rarely gray, with felt-like indumentum, hairs densely matted; hairs when examined under magnification of about 50 diameters are seen to be smooth or with only a few scattered tubercles.
c. subsp. *radiata*

1a. *Hydrangea arborescens* Linnaeus subsp. *arborescens*.

Hydrangea arborescens Linnaeus, Species Plantarum, 937. 1753.

Hydrangea vulgaris Michaux, Flora Boreali-Americana, 1:268. 1803. A specimen under this name, without locality or other data, in the Michaux Herbarium of the Natural History Museum, Paris, may be the type.

Hydrangea arborescens var. *vulgaris* (Michaux) Seringe in DeCandolle, Prodromus, 4:14. 1830.

Hydrangea arborescens var. *kanauchana* Millspaugh, Preliminary Catalogue of the Flora of West Virginia, 363. 1892. Type from West Virginia, Millspaugh 291 (WVA).

Hydrangea arborescens var. *australis* Harbison, American Midland Naturalist, 11:255. 1928. Type from Union Springs, Alabama, Harbison June 18, 1902. (Biltmore Herb. No. 1339i, US.)

(Note: A number of additional synonyms, listed by Rehder in the Bibliography of Cultivated Trees and Shrubs, pp. 199–200 (1949) under *Hydrangea arborescens*, are not included here. These could not be verified; in some cases, the names were based on cultivated plants and the type specimens were not designated; in other cases, the type specimens could not be located.)

Lower leaf surface glabrous or nearly so, with hairs, when present, along midrib; individual hairs conspicuously tubercular, 0.3–1 mm. long, 10–25 microns wide; sterile flowers often not present.

TYPE LOCALITY: Virginia. Type collection: "Dr. Clayton, ex America, An. 1734, num. 79" (BM).

ILLUSTRATIONS:

The Botanical Magazine, vol. 13, table 437. 1799.

Gleason, H. A. Illustrated Flora of the Northeastern United States and Adjacent Canada, 2: 275. 1952.

New Flora and Silva, 4: figure 79, 1932 (habit); 9: figure 34, 1937 (habit), both as *Hydrangea arborescens grandiflora*.

DISTRIBUTION: Southern New York southward through the Appalachian Mountains to the coastal plain of central Alabama, westward to the Ozarkian Plateaus. ALABAMA: Bullock, Cullman, DeKalb, Etowah, Hale, Henry, Lee, Madison, Montgomery, St. Clair, Tuscaloosa, and Winston counties. ARKANSAS: Baxter, Benton, Clay, Carroll, Craighead, Crawford, Faulkner, Independence, Logan, Marion, Perry, Pike, Polk, Pope, Saline, Washington, and Yell counties. DISTRICT OF COLUMBIA. GEORGIA: Bartow, Catoosa, Clarke, Clay, Cobb, DeKalb, Fannin, Floyd, Fulton, Gilmer, Gordon, Gwinnet, Habersham, Hall, Hancock, Lumpkin, Madison, Pickens, Rabun, Rockdale, Stephens, Towns, and White counties. ILLINOIS: Champaign, Jackson, Johnson, Madison, Randolph, Richland, Shelby, and Union counties. INDIANA: Cass, Clinton, Crawford, Floyd, Harrison, Howard, Huntington, Jefferson, Knox, Lawrence, Marion, Martin, Monroe, Morgan, Ohio, Orange, Owen, Parke, Perry, Putnam, Ripley, Scott, Vermillion, and Warren counties. KENTUCKY: Allen, Anderson, Bath, Bell, Boyd, Boyle, Breathitt, Carter, Casey, Christian, Daviess, Edmonson, Estill, Fayette, Greenup, Grayson, Hancock, Harlan, Jefferson, Jessamine, Johnson, Letcher, Lyon, Madison, McCreary, Ohio, Pike, Union, Warren, and Wolfe counties. LOUISIANA: West Feliciana Parish. MARYLAND: Allegany, Cecil, Frederick, Harford, Howard, Montgomery, and Prince Georges counties. MISSISSIPPI: Tishomingo and Wayne counties. MISSOURI: Barry, Butler, Callaway, Christian, Crawford, Dent, Dunklin, Franklin, Gasconade, Greene, Hickory, Howell, Iron, Jefferson, McDonald, Miller, Newton, Oregon, Ozark, Pulaski, Ripley, St. Charles, St. Genevieve, Shannon, Stoddard, Stone, Taney, Wayne, Webster, and Wright counties. NEW JERSEY: Burlington, Mercer, and Warren counties. NEW YORK: Chemung, Steuben, and Tioga counties. NORTH CAROLINA: Alexander, Alleghany, Ashe, Avery, Buncombe, Cherokee, Craven, Cumberland, Durham, Forsyth, Graham, Haywood, Jackson, Iredell, Macon, Madison, Montgomery, Orange, Polk, Rockingham, Stanley, Stokes, Surry, Swain, Transylvania, Wake, Watauga, Wilkes, Yadkin, and Yancey counties. OHIO: Adams, Belmont, Butler, Columbiana, Fairfield, Green, Hamilton, Jefferson, Lawrence, Meigs, Pike, Ross, and Scioto counties. OKLAHOMA: Cherokee, Delaware, Johnston, LeFlore, and McCurtain counties.

PENNSYLVANIA: Allegheny, Blair, Bradford, Bucks, Butler, Cameron, Centre, Chester, Clearfield, Elk, Fayette, Franklin, Fulton, Lancaster, Lehigh, Luzerne, Lycoming, Mifflin, Monroe, Montgomery, Northampton, Perry, Philadelphia, Schuylkill, Snyder, Sullivan, and Westmorland counties. SOUTH CAROLINA: Oconee County. TENNESSEE: Bedford, Blount, Campbell, Carter, Cheatham, Cocke, Coffee, Cumberland, Davidson, Fentress, Franklin, Grainger, Hamilton, Knox, Pickett, Rhea, Sevier, Shelby, Sullivan, Unicoi, and Washington counties. VIRGINIA: Arlington, Augusta, Bedford, Botetourt, Carroll, Fairfax, Fauquier, Giles, Green, Greensville, Isle of Wight, James City, Loudoun, Louisa, Madison, Mecklenburg, Montgomery, Middlesex, Page, Patrick, Rappahannock, Roanoke, Rockbridge, Rockingham, Scott, Shenandoah, Smyth, Southampton, Surry and York counties. WEST VIRGINIA: Barbour, Boone, Braxton, Cabell, Calhoun, Doddridge, Fayette, Grant, Greenbrier, Hampshire, Harrison, Jefferson, Kanawha, Marion, Marshall, Mercer, Mineral, Monongalia, Monroe, Morgan, Nicholas, Ohio, Pendleton, Preston, Raleigh, Randolph, Ritchie, Summers, Taylor, Tucker, Tyler, Upshur, Wayne, Webster, Wetzel, and Wood counties.

1b. *Hydrangea arborescens* subsp. *discolor* (Seringe)

McClintock, Journal Arnold Arboretum, 37:373. 1956¹.

Hydrangea arborescens var. *discolor* Seringe in DeCandolle, Prodrumus, 4:14. 1830.

Hydrangea arborescens var. *Deamii* St. John, Rhodora, 23:208. 1921. Type from Jackson County, Indiana, *Deam* 28122 (isotype A).

Hydrangea arborescens var. *Deamii* f. *acarpa* St. John, l. c. Type from Montier, Shannon County, Missouri. *Bush* 6116 (holotype GH, isotypes MO, US).

Hydrangea Ashei Harbison, American Midland Naturalist, 11:256. 1928. Type material said to be from Montgomery County, Arkansas, collected by Ashe, but no actual specimen was cited. Placed here because the leaves were described as being pubescent.

Hydrangea cinerea Small, Bulletin Torrey Botanical Club, 25:148. 1898. In part. Small cited five syntypes. Of these *Lamson-Scribner*, June 29, 1890 (NY, US), and *Kearney*, July 16, 1894 (US, NY, MO), both collected at White Cliff Springs, Tennessee, and *Small*, August 7-12, 1895 (A, BH), Ringgold, Catoosa County, Georgia, are subsp. *discolor*.

Lower leaf surface velutinous, pilose, or tomentose, usually grayish; individual hairs conspicuously tubercular, 0.3-1 mm. long, 10-25 microns wide; sterile ray flowers present or absent.

Type collection of *Hydrangea arborescens* var. *discolor*: A cultivated specimen collected by Seringe in 1824 (G).

¹ Herbarium specimens belonging to this taxon were annotated before the writer had seen the specimen typifying Seringe's varietal epithet. Because there was some doubt as to the proper application of this name previous to this time a combination based on St. John's var. *Deamii* was used to annotate the specimens studied earlier.

DISTRIBUTION: Occurring with subsp. *arborescens* except in the north-eastern part of the range of that subspecies. ALABAMA: Bibb, Calhoun, Clay, De Kalb, Jackson, Jefferson, Lauderdale, Madison, Marshall, and Tuscaloosa counties. ARKANSAS: Baxter, Benton, Carroll, Cleburne, Crawford, Cross, Garland, Hot Springs, Newton, Pulaski, Phillips, Poinsett, Pope, St. Francis, Stone, Van Buren and White counties. GEORGIA: Catoosa, Cobb, Dade, Walker and Whitfield counties. ILLINOIS: Calhoun, Champaign, Jackson, Jersey, Johnson, Peoria, Pope, St. Clair, Vermillion, and Williamson counties. INDIANA: Bartholomew, Brown, Gibson, Jackson, Knox, Morgan, Monroe, Perry, Posey, and Tippecanoe counties. KENTUCKY: Livingston and Union counties. MISSOURI: Cape Girardeau, Carter, Dallas, Jefferson, Madison, Newton, Oregon, Ozark, Phelps, Pike, Reynolds, Ripley, St. Genevieve, St. Louis, Scott, Shannon, Stoddard and Washington counties. OKLAHOMA: LeFlore County. TENNESSEE: Blount, Carroll, Davidson, Decatur, Franklin, Grundy, Hamilton, Marion, Monroe, Obion, Polk, Roane and Van Buren counties.

1c. *Hydrangea arborescens* subsp. *radiata* (Walter) McClintock, Journal Arnold Arboretum, 37: 373. 1956.

Hydrangea radiata Walter, Flora Caroliniana, 251. 1788.

Hydrangea nivea Michaux, Flora Boreali-Americana, 1: 268. 1803. A specimen under this name, without locality or other data, in the Michaux Herbarium, Natural History Museum, Paris, is doubtless the type.

Hydrangea nivea Michaux var. *conformis* Seringe in DeCandolle, Prodrromus, 4: 14. 1830.

Hydrangea cinerea Small, Bulletin Torrey Botanical Club, 25: 148. 1898. In part. Small cited five syntypes. Of these *Curtiss 833* (June, 1882) (MO, US, GH, UC, BM, W, G, K), Chilhowee Mountains, Blount County, Tennessee, and *Kearney, June 24, 1893* (NY), Chilhowee Gap, Blount County, Tennessee, are *H. arborescens* subsp. *radiata*.

Lower leaf surface covered with a conspicuous white felt-like indumentum, occasionally a grayish tomentum; individual hairs either smooth (without any tubercules), 1–3 mm. long, 5–10 microns wide, or with a few scattered tubercules, 1–3 mm. long, 5–20 microns wide; sterile flowers usually present.

TYPE LOCALITY of *Hydrangea radiata*: "Carolina." Type collection: *Walter s.n.* (BM).

DISTRIBUTION: Occurring with the other two subspecies in the southern section of the Blue Ridge Mountains, extending to the piedmont area in the vicinity of the Seneca River in the northwestern corner of South Carolina.

Plants with indumentum composed of smooth hairs: GEORGIA: Rabun County. NORTH CAROLINA: Buncombe, Graham, Henderson, Jackson,

Macon, Madison, Polk, Swain, and Transylvania counties. SOUTH CAROLINA: Anderson, Greenville, Oconee, and Pickens counties. TENNESSEE: Blount County.

Plants with indumentum composed of inconspicuously tubercular hairs: NORTH CAROLINA: Buncombe, Henderson, Macon, Polk, Swain, and Transylvania counties. TENNESSEE: Blount County.

VARIATION IN *Hydrangea arborescens*

Variation in *Hydrangea arborescens* involves the kind and amount of vesture on the lower leaf surface, the presence or absence of sterile peripheral flowers, and the size and shape of the leaves. The flower parts show no variation.

The vesture characters of the lower leaf surface have been used to divide the species into subspecies as follows:

1. Lower leaf surface glabrous or nearly so, with only a few scattered hairs along the midrib (plate 1, figure 1). Subsp. *arborescens*.

2. Lower leaf surface pubescent with erect or spreading, straight, rather firm hairs which vary in amount from sparsely scattered to dense enough to cover the surface and form a gray tomentum (plate 1, figures 2 and 3; plate 2, figure 3). The hairs are covered with numerous tubercles, giving them a roughened appearance (plate 3, figure 4), and are 0.5–1 mm. long and 10–25 microns wide. These hairs are found in subsp. *discolor*. The few hairs along the midveins of subsp. *arborescens* have also these same dimensions and markings.

3. Lower leaf surface with intertwined fine woolly hairs, usually very dense and forming a white, or rarely gray, felt-like indumentum (plate 1, figure 4). The hairs have a smooth surface (plate 3, figure 1) and are 1–3 mm. long and 5–10 microns wide. Subsp. *radiata*.

4. Lower leaf surface with indumentum resembling that of 3 above, except for its gray color (plate 2, figure 2) and with hairs which differ in having a few scattered tubercles (plate 3, figures 2 and 3). The hairs are 1–3 mm. long and 5–20 microns wide. These hairs appear more like the hairs of subsp. *radiata* and therefore the individuals having them are included in this subspecies.

The geographical distribution of the three subspecies is given on Map 2. It is seen from this map that subsp. *arborescens* is the most widespread of the three; that subsp. *discolor* occurs in the western and southeastern, but not in the northeastern part of the range of subsp. *arborescens*; and that subsp. *radiata* occurs only in the southeastern part of ranges of the other subspecies, which is the southern Appalachian Mountains. The distribution of the three subspecies in the southern Appalachians is shown on Map 3. In this area occur the two forms of subsp. *radiata*, the one having smooth hairs and the other having hairs with scattered tubercles.

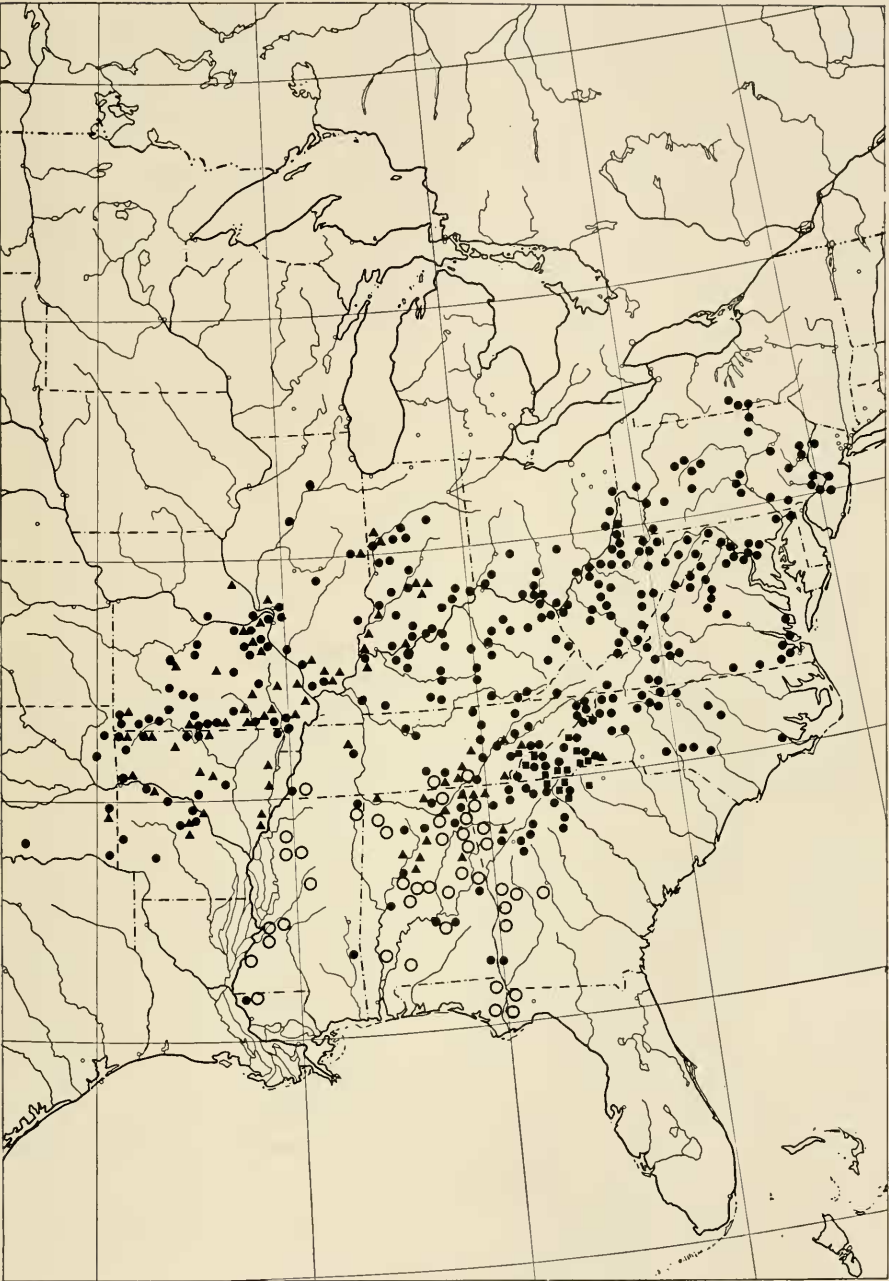
Here also occur individuals of subsp. *discolor* having both "sparse" and "dense" pubescence, as well as subsp. *arborescens*.

Sterile flowers are present in the inflorescences of some individuals and absent in others. There is evidence to show from herbarium specimens that their presence is associated in part with type of pubescence and in part with geographic range. Of 231 individuals of subsp. *arborescens* in the eastern part of its range, from Virginia to South Carolina, 65, or 27 per cent, had sterile flowers, while in the western part of its range, from Tennessee and Kentucky to Missouri and Arkansas, of 243 individuals, 167, or 69 per cent, had sterile flowers. In the western part of the range of subsp. *discolor* (Missouri, Arkansas, Indiana, Illinois, and Ohio), of 87 individuals, 14, or 17 per cent had sterile flowers, but in the eastern part of its range, Georgia, Alabama, and Tennessee, where the pubescence is "sparse" to "dense," of 39 individuals, 36, or 92 per cent, had sterile flowers. In subsp. *radiata*, 50 individuals of the form having smooth hairs were examined, and 49, nearly 100 per cent, had sterile flowers, and of the form having a few tubercles on its hairs, 9 out of 19, or 47 per cent, had sterile flowers.

Since all of the subspecies are found in the southern Appalachian Mountains, and often more than one have been found by different collectors at, or near, the same locality, it seemed of interest to determine whether more than one subspecies occur together, and if so, whether the form of subsp. *radiata* with scattered tubercles on its hairs would be found. In the summer of 1948, the writer visited this region and collected *Hydrangea* material in about 50 localities. It was found that for the most part the plants were uniform at a given locality. In only two localities were there more than one subspecies. In Madison County, North Carolina, about 4½ miles west of Walnut Gap, there were typical plants of both subsp. *arborescens* and subsp. *radiata*. The other locality was in the Pisgah National Forest, near White Pine Annex Campground, Transylvania County, North Carolina. The three subspecies were in this locality along with several atypical individuals. No. 48-59B (see plate 2, figure 2) was like the one previously referred to subsp. *radiata*. There were several other individuals (Nos. 48-61B, 48-59A, see plate 2, figure 1, and No. 48-60, see plate 1, figure 5) in which the hairs were short (0.5-1 mm.) and had

MAP 2. Distribution in the eastern United States of

- *Hydrangea quercifolia*
- *Hydrangea arborescens*
- subsp. *arborescens*
- ▲ subsp. *discolor*
- subsp. *radiata*



numerous tubercles as in subsp. *discolor*, but their width was less (5–20 microns) than is typical for this subspecies. Another individual, No. 48–61C, placed in subsp. *arborescens* because of being nearly glabrous, had a few scattered hairs along the veins which were like those of the individuals of subsp. *discolor* just described.

A search for similar atypical individuals in other localities in the Pisgah Forest area was not successful. It would appear that such individuals are rare. Dunean (*Castanea* 15:153, 1950) reported finding subsp. *arborescens* and *radiata* growing together in Rabun County, Georgia, but he found no “intermediates” in a large number of plants inspected. Perhaps if the localities where those individuals of subsp. *radiata* having inconspicuously tuberculate hairs have been found were searched, other intermediates would turn up. However, it would appear that intermediates are not common and those few which have appeared have not caused the character of the populations to change.

2. *Hydrangea quercifolia* Bartram, *Travels*, xviii, *nom.*, 382, t. 6, descr., 408, *nom.* 1791; ed. 2, xii, 380, t. 6, 406, 1792.² *Species Plantarum*, ed. 4, C. L. Willdenow, 2: 634. 1799³.

Hydrangea radiata Smith, *Icones Pictae Plantarum rariorum*, t. 12. 1791. *Non* Walter, 1788.

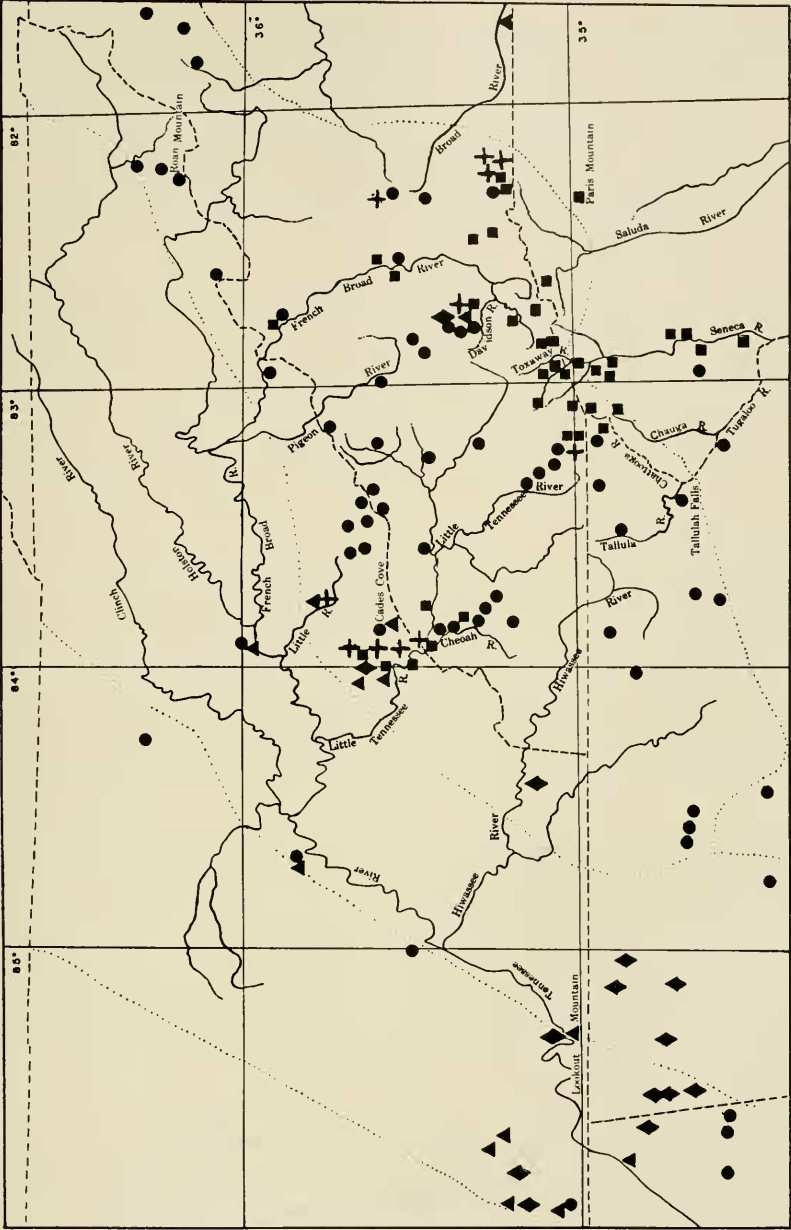
Stout erect shrub, much branched from base, 1–2 m. tall; young branchlets and petioles densely tomentose with long, fine, reddish hairs; branches of inflorescence pilose with short, coarse hairs; leaves suborbicular or oval in outline, 8–25 cm. long, mostly 5-lobed, the lobes coarsely serrate, petioles one-eighth to one-third as long as blades; upper leaf surface gla-

² According to Merrill (*Bartonia*, 23:10–35, 1945), the citation of *H. quercifolia* given in *Index Kewensis* is not correct. The citation here is Merrill's correction.

³ Because of the doubt which is attached to Bartram's *Travels* as a legitimate place to begin nomenclature, Willdenow's publication may be considered to be the earliest valid one for this name. See Merrill, *l. c.* pp. 17 and 27.

MAP 3. Distribution in the southern Appalachian Mountains
of *Hydrangea arborescens*

- subsp. *arborescens*
- subsp. *discolor*
- ▲ sparsely pubescent
- ◆ tomentose
- subsp. *radiata*
- indumentum white and hairs smooth
- ✚ indumentum gray and hairs inconspicuously tubercular



brous; lower leaf surface pilose or tomentose with two kinds of hairs—short, coarse, tubercular ones, and longer, fine, smooth ones which form an intertwining network; inflorescence a compound, much branched cluster, pyramidal in shape, 15–25 cm. long; fertile flowers white, very numerous; hypanthium 1–1.5 mm. long; calyx lobes 5, deltoid, 0.5–0.8 mm. long; petals oblong, acute, concave, 2–2.5 mm. long; stamens 10, 3–6 mm. long; styles 2, 3, or 4, 1–1.4 mm. long, somewhat thickened toward apex; capsules 1.5–2.5 mm. long, 2–2.5 mm. wide at apex, apex truncate, ribs 7 or 8, inconspicuous; styles 1.2–1.5 mm. long; seeds elliptical, 0.7–0.8 mm. long, 0.3–0.4 mm. wide, prominently striate, blunt at each end; sterile flowers present, usually a single one terminating each lateral branch of the inflorescence, four-lobed, lobes orbicular, 10–15 mm. in diameter. (See plate 4, figure 2.)

TYPE LOCALITY: GEORGIA: Crawford County, Sweet Water Brook = Knoxville Branch (see Merrill, *Bartonia* 23: 27, 1945). TYPE COLLECTION: W. Bartram s. n. (holotype BM).

ILLUSTRATIONS:

Curtis's Botanical Magazine, table 975, 1806.

New Flora & Silva 4: fig. 80. 1932 (habit).

Gleason, H. A. 1952. Illustrated Flora of the Northeastern United States and Adjacent Canada, 2: 275.

DISTRIBUTION: Southeastern United States, on the piedmont and coastal plain of western Georgia, Alabama, and Mississippi. (See Map 2.)

ALABAMA: Blount, Calhoun, Clarke, Conecuh, Cullman, Dallas, DeKalb, Etowah, Franklin, Jackson, Jefferson, Marshall, Shelby, St. Clair, Tallapoosa, Tuscaloosa, and Winston counties. FLORIDA: Calhoun, Gadsden, Jackson

PLATE 1. Vesture types in *Hydrangea arborescens*.

Figure 1. Subsp. *arborescens*. Lower leaf surface glabrous except for few scattered hairs along veins. (from McClintock 48–44)

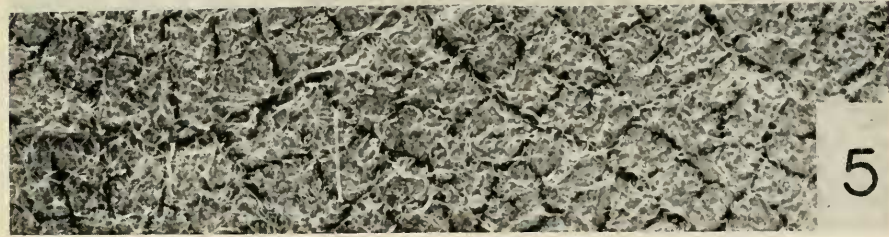
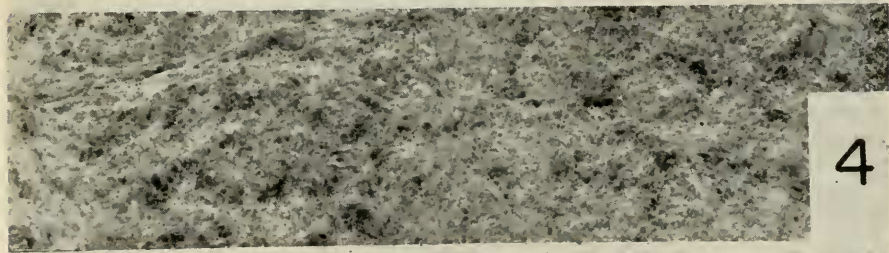
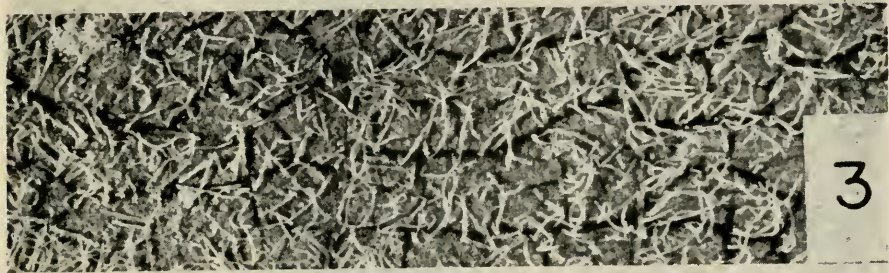
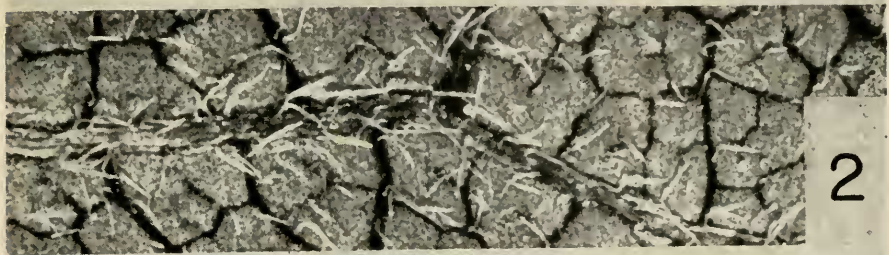
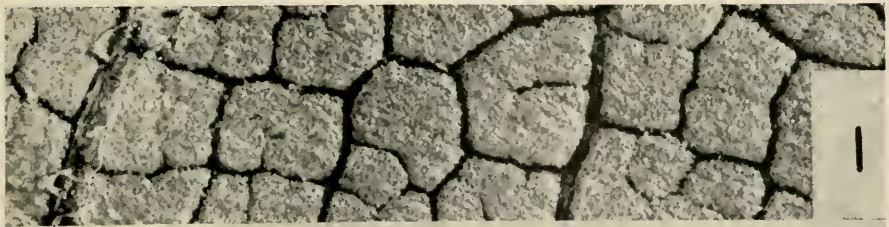
Figure 2. Subsp. *discolor*. Lower leaf surface sparsely pubescent. (from Palmer 12640)

Figure 3. Subsp. *discolor*. Lower leaf surface with slightly more hairs than in figure 2. (from Deam 2248)

Figure 4. Subsp. *radiata*. Lower leaf surface covered with white felt-like indumentum. (from McClintock 48–53)

Figure 5. Subsp. *discolor*. Lower leaf surface moderately pubescent with hairs finer than those in figure 3. (from McClintock 48–60)

The photographs in this plate and in Plate 2 were taken by Richard Johnson. Magnification in all figures on both plates is 19×.



and Liberty counties. GEORGIA: Bibb, Chattahoochee, Clarke, Clay, Crawford, Dade, Decatur, Early, Floyd, Harris, Heard, Merriwether, Polk, Randolph, Stewart, Talbot, Taylor, and Upson counties. LOUISIANA: East Feliciana and West Feliciana parishes. MISSISSIPPI: Adams, Attala, Copia, Grenada, Hinds, Holmes, Itawamba, Tallahatchie, Tishomingo, and Warren counties. TENNESSEE: Lincoln, Marion, and Shelby counties.

DISCUSSION: *Hydrangea quercifolia* is remarkably uniform throughout its range. It is characterized by its pyramidal inflorescence and its lobed leaves, by which characters it is distinguished from *H. arborescens*. In geographic distribution these two species differ, although they overlap in part in the southern part of the range of *H. arborescens*. *Hydrangea quercifolia* is found chiefly in the area of the piedmont and coastal plain of western Georgia, Alabama, and Mississippi. *Hydrangea arborescens* subsp. *arborescens* and subsp. *discolor* occur infrequently in this area.

Subsection 2. ASPERAE

Hydrangea, sect. *Euhdrangea* Maximowicz, subsect. *Asperae* Rehder, *Plantae Wilsonianae*, 1:39. 1911.

Hydrangea, sect. *Euhdrangea* Maximowicz, subsect. *Piptopetalae* Maximowicz, *Mémoires Académie impériale des Sciences de St. Pétersbourg*, ser. 7, 10(16):8 (Revisio *Hydrangearum Asiae Orientalis*), 1867. In part.

Hydrangea, subgenus *Euhdrangea*, sect. *Japonico-sinensis*, subsect. *Piptopetalae* Schneider, *Handbuch der Laubholzkunde*, 388, 1905. In part.

Flowers white or blue; ovary inferior; capsule truncate at apex; styles free to their bases; seeds caudate. Chinese and Japanese species.

TYPE SPECIES: *Hydrangea aspera* Don.

PLATE 2. Vesture types in *Hydrangea arborescens* and *Hydrangea aspera*.

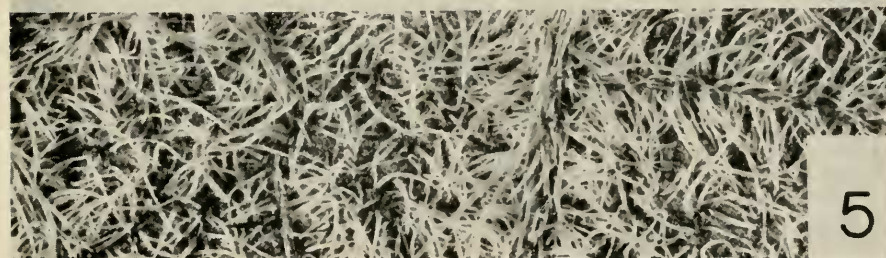
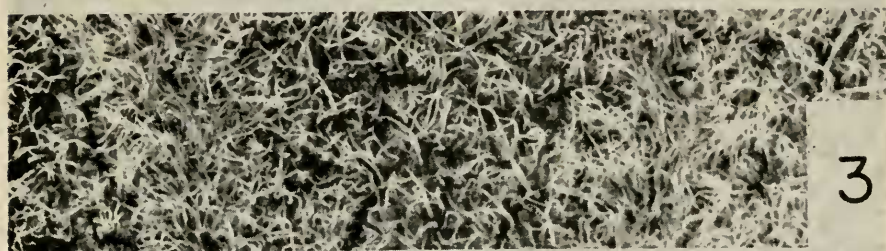
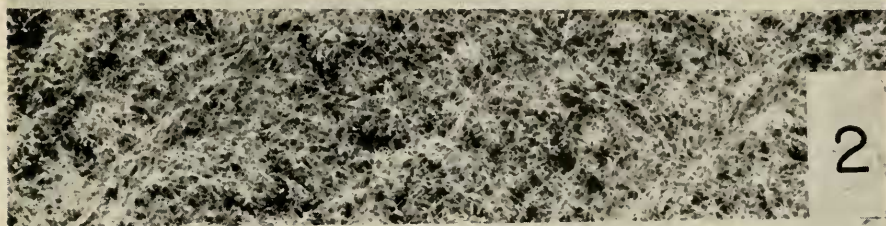
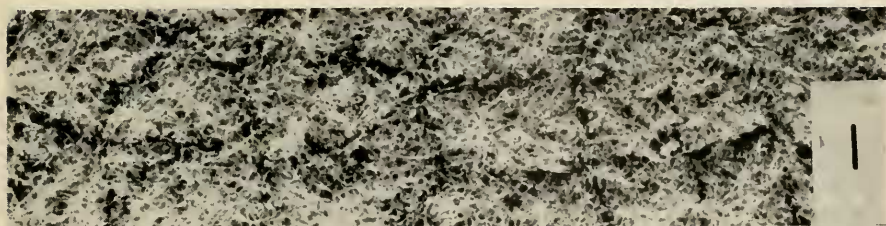
Figure 1. *Hydrangea arborescens* subsp. *discolor*. Lower leaf surface moderately pubescent with hairs somewhat finer, longer and more dense than those on Plate 1, figure 5. (from McClintock 48-59A)

Figure 2. *Hydrangea arborescens* subsp. *radiata*. Lower leaf surface covered with gray indumentum, hairs not as dense as in Plate 1, figure 4, and having scattered tubercles. (from McClintock 48-59B)

Figure 3. *Hydrangea arborescens* subsp. *discolor*. Lower leaf surface gray tomentose. (from McClintock 48-82.)

Figure 4. *Hydrangea aspera* subsp. *strigosa*. Hairs straight, appressed along raised veins. (from Fang 15568)

Figure 5. *Hydrangea aspera* subsp. *aspera*. Hairs tending to be erect and spreading. (from Fang 19721)



3. *Hydrangea sikokiana* Maximowicz, Bulletin scientifique Académie impériale des Sciences de St. Pétersbourg, 31: 42. 1887.

Shrub, 1–2 m. tall; branchlets, inflorescence and pedicels pubescent with upwardly appressed hairs 0.5–1 mm. long; leaves pinnately lobed with 4 to 6 lobes, 8–21 cm. long, 8–20 cm. wide, lower surface pubescent along veins and veinlets with hairs 1–1.5 mm. long, upper surface with scattered hairs along veins; petioles 2–18 cm. long, pubescent; inflorescence a flat-topped, compound, several-branched cluster, 12–30 cm. across; bracts few, scattered through inflorescence, lanceolate to ovate, 10–30 mm. long, pubescent as leaves; fertile flowers purplish; hypanthium 1–1.6 mm. long; calyx lobes 5, broadly deltoid, 0.5 mm. long; petals 5, 2–4 mm. long, 1.5–2 mm. wide, truncate at base; stamens 10, rarely 8 or 9, 3.5–5.5 mm. long; styles 2, 1–1.5 mm. long; ovary inferior; capsule 2–3 mm. long, styles 1.5–2 mm. long; seeds elliptical, 1 mm. long, tapering at each end into minute tail-like extensions; sterile flowers always present, purplish, 4-lobed, lobes rounded, 1–3 cm. in diameter. (See plate 5, figure 1.)

TYPE LOCALITY: Japan, Honshu Island, Kii Province (now Wakayama and Mie prefectures). Type collection: *Tanaka*. Specimen not seen by the writer.

DISTRIBUTION: Woods and mixed forests on Honshu and Kyushu islands in Japan, from 100 to 1,000 meters. (See Map 4.) JAPAN. HONSHU ISLAND: Nara Prefecture: Tonomine, Mt. Odaigahara. Wakayama Prefecture: Mt. Koya. KYUSHU ISLAND: Oita Prefecture: Bungo. Kagoshima Prefecture: Mt. Hirishima. Kumamoto Prefecture: Hitoyoshichi.

DISCUSSION: *Hydrangea sikokiana* is distinguished from *H. involucrata*, the only other closely related Japanese species, by its pinnately lobed leaves. The American species, *H. quercifolia*, and *H. sikokiana* are the only species in the genus which have lobed leaves.

PLATE 3.

Surface appearance of hairs from lower leaf surfaces of *Hydrangea arborescens*.

Figure 1. Smooth hairs of subsp. *radiata*. (from McClintock 48–27)

Figure 2. Hairs with very few tubercles from subsp. *radiata*. (from Correll 3717)

Figure 3. Hairs with few tubercles from subsp. *radiata*. (from Davis 7683)

Figure 4. Hairs with numerous, conspicuous tubercles from subsp. *discolor*. (from Palmer 35469)

Drawings made with a camera lucida. Magnification 350×.

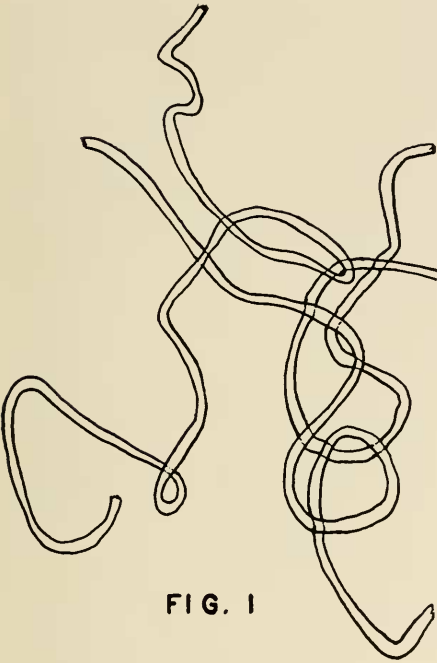


FIG. 1

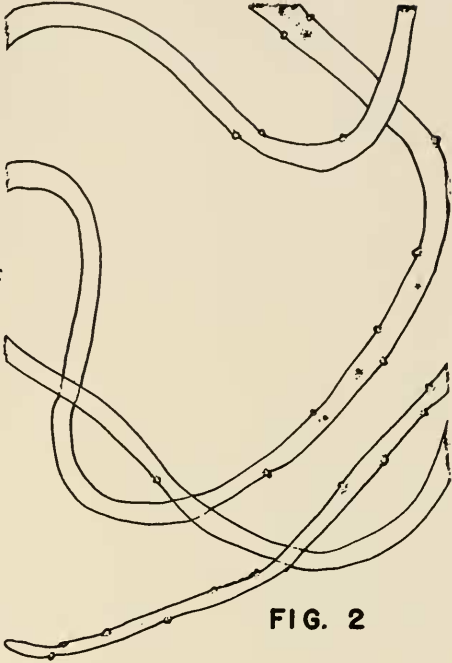


FIG. 2

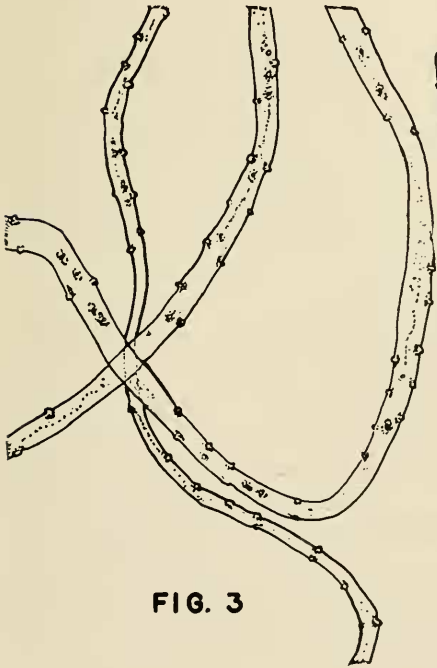


FIG. 3

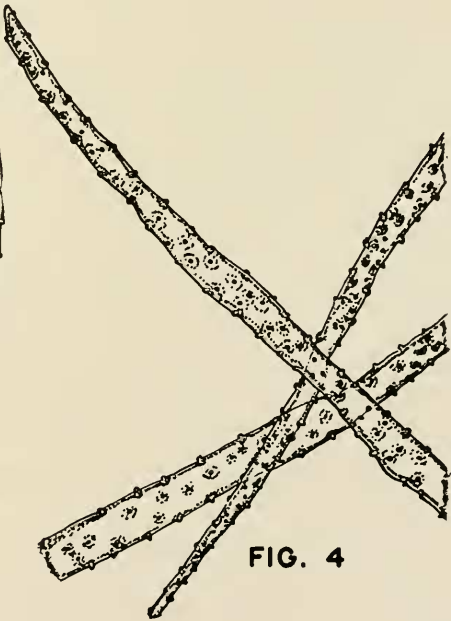


FIG. 4

4. *Hydrangea involucrata* Siebold, Nova Acta: Academia (caesarea)
Leopoldino-Carolina, 14(2): 691. 1829.

Hydrangea longifolia Hayata, Journal, College of Science, Imperial University, Tokyo, 25(19): 91. 1908. Type from Formosa, Kawakami & Nakahara 690, not seen, photo CAS.

Shrub, 1-2 m. tall; branchlets, inflorescence and pedicels pubescent with upwardly appressed hairs 0.5 mm. long; leaves ovate, 10-26 cm. long, 5-17 cm. wide, their length 1.5 to 2.5 times their width; both surfaces pubescent with appressed hairs; petiole 1.5-8 mm. long; inflorescence rounded, compound, many-branched; involueral bracts subtending the inflorescence, 1.5-2.5 cm. long, broadly obovate, pubescent with upwardly appressed white hairs on outside, glabrous on inside, caducous, leaving a row of scars at base of inflorescence when falling; in addition, a few bracts, ovate or lanceolate in shape, are scattered through the inflorescence; fertile flowers lavender, hypanthium 1.2-1.5 mm. long; calyx lobes 5, deltoid, 0.2-0.6 mm. long; petals 5, 2-3 mm. long, truncate at base; stamens 10, rarely 11 or 12, 3.5-6 mm. long; ovary inferior; styles 2 or 3, 1-2 mm. long; capsules 3-4 mm. long, pubescent, styles 2-2.5 mm. long; seeds elliptical, 0.8-1 mm. long, tapering at each end into minute tail-like extensions; sterile flowers always present, lavender, 4-lobed, lobes rounded, 1-3 cm. in diameter. (See plate 5, figure 5.)

PLATE 4. Flowers and capsules of some American species of *Hydrangea*.

Figure 1. *Hydrangea arborescens*. a. flower (without petals and some of stamens. Biltmore herb. 1339c). b. capsule (Biltmore herb. 8212d).

Figure 2. *Hydrangea quercifolia*. a. flower. b. capsule.

Figure 3. *Hydrangea asterolasia*. a. flower (Skutch 3342). b. capsule (A. Smith H470).

Figure 4. *Hydrangea peruviana*. a. flower (Allen 534). b. capsule (Standley 39080).

Figure 5. *Hydrangea Mathewsii*. Flower (Mathews 3051).

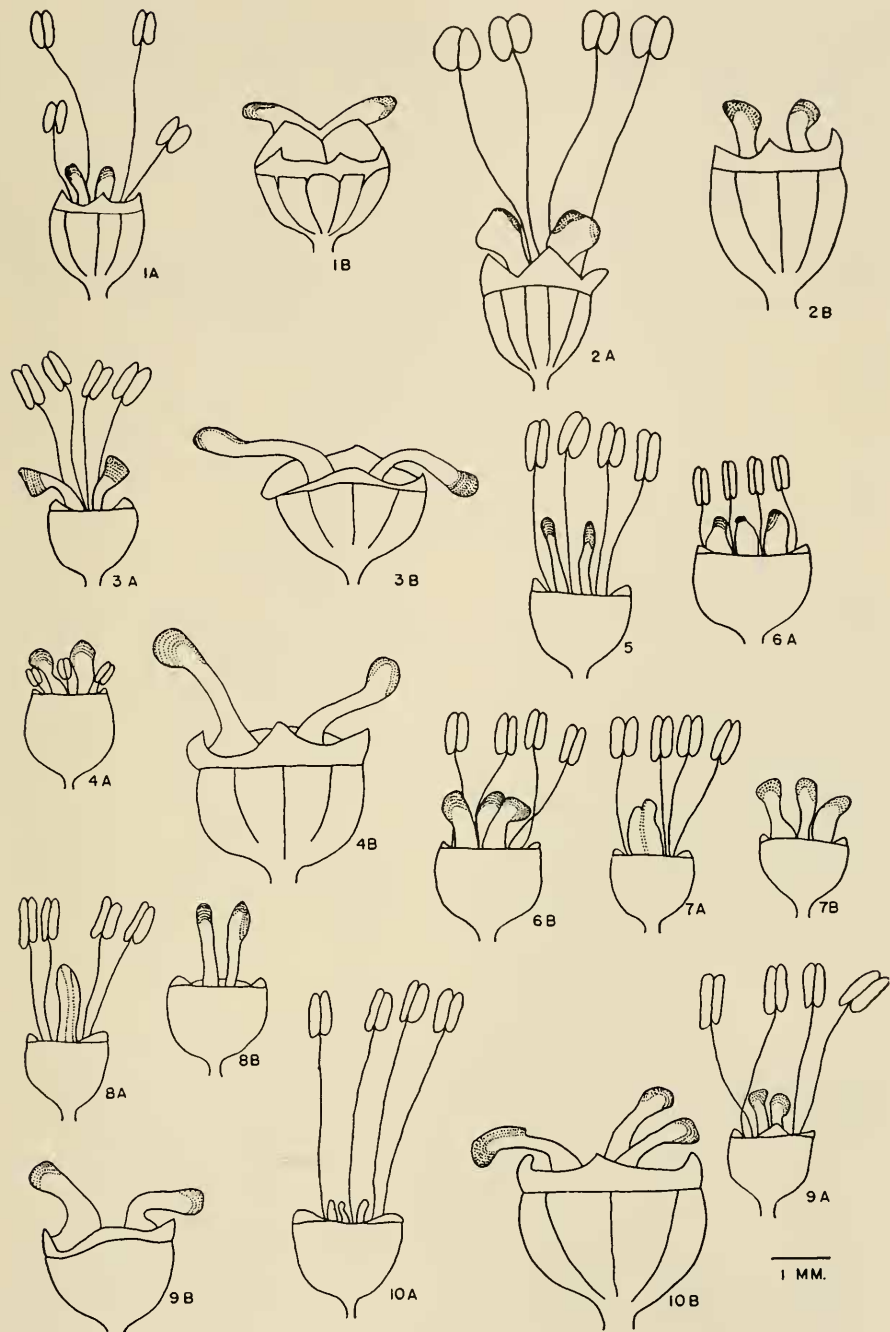
Figure 6. *Hydrangea Preslii*. a. flower (Weberbauer 6776). b. flower (Skutch 2630).

Figure 7. *Hydrangea diplostemonia*. a. flower (Spruce 4328). b. young capsule (Spruce 4328).

Figure 8. *Hydrangea tarapotensis*. a. flower (Smith 2627). b. young capsule (Lawrence 775).

Figure 9. *Hydrangea integrifolia*. a. flower (Clemens June 1924). b. capsule (Wilson 9691).

Figure 10. *Hydrangea serratifolia*. a. flower (Morton Dec. 3, 1906). b. capsule (Sargent Jan. 12, 1906).



TYPE LOCALITY: Japan. Type collection: Collected in Japan by von Siebold. The specimens collected in Japan by von Siebold are in the Rijksherbarium in Leiden. Presumably the type of *H. involucrata* is there but the writer has not seen it.

ILLUSTRATION: Siebold and Zuccarini. Flora Japonica, plates 63 and 64. 1839 or 1840.

DISTRIBUTION: Woods and mixed forests on Honshu Island in Japan, from near sea level to 1,500 meters, and on Formosa. JAPAN. HONSHU ISLAND: Chiba Prefecture: Owari, Kiyozumi-yama. Fukushima Prefecture: Mt. Haguro. Gifu Prefecture: Norikura, Washiga-take. Gumma Prefecture: Ikaho. Kanagawa Prefecture: Yokohama, Miyanoshita, Hakone Mts., Kamakura, Mt. Takao. Nagano Prefecture: Usui-toge, Mt. Izuna, Mt. Tsubakura, Kuramoto, Kiso near On-take-san, Asamayama. Shiga Prefecture: Shinano. Tochigi Prefecture: Nikko. Tokyo Prefecture: Tokyo, Mt. Takao, Hachijo. Yamanashi Prefecture: Motsuko. (See Map 4.)

DISCUSSION: *Hydrangea involucrata* bears a close resemblance to *H. aspera* in flower and fruit structures, and in the shape of the leaves. The two species may be distinguished by the tomentose capsules and the involucreal bracts of *H. involucrata*. These bracts which envelop the unopened inflorescence resemble those found in the section Cornidia.

The distribution of *Hydrangea involucrata* as listed above includes localities from Japan only. The species, however, occurs in Formosa as indicated by a specimen collected by Kawakami and Nakahara at Taito on the southeast coast in January 1906. This specimen, the type of *Hydrangea longifolia* Hayata, was not seen by the writer. A photograph of the specimen shows the scars left by deciduous involucreal bracts, the presence of which identifies it with *H. involucrata*.

PLATE 5. Flowers and capsules of some Asiatic species of *Hydrangea*.

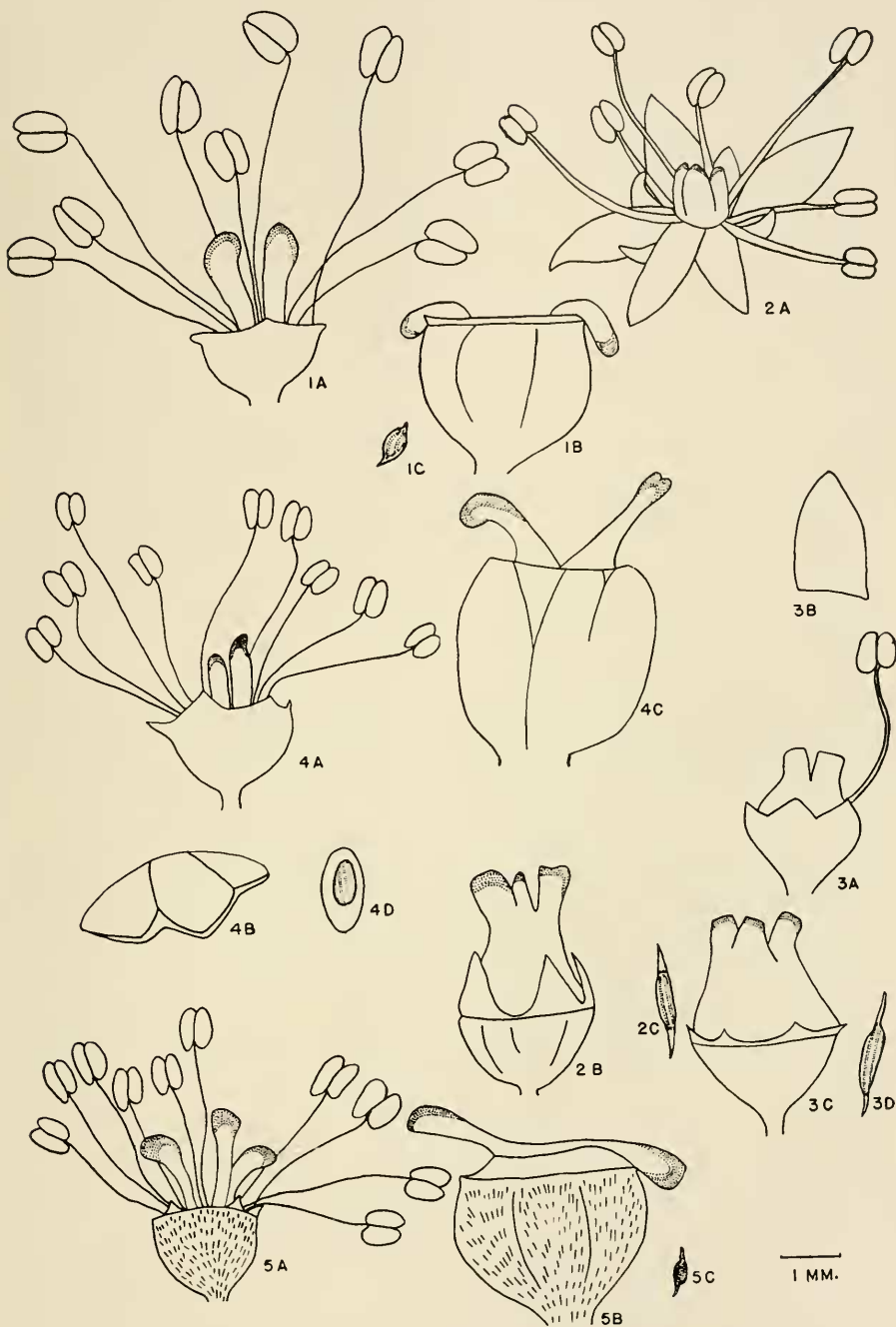
Figure 1. *Hydrangea sikokiana*. a. flower (Sakurai August 16, 1909). b. capsule (Komeda E53). c. seed (Komeda E53).

Figure 2. *Hydrangea heteromalla*. a. flower (Wilson 2184). b. capsule (Li 23). c. seed (Li 23).

Figure 3. *Hydrangea paniculata*. a. flower (Chung & Sun 469). b. single petal. c. capsule (Canton Christian College herb. no. 8738). d. seed (as preceding).

Figure 4. *Hydrangea anomala*. a. flower (Wilson 4901). b. united petals or calyptra (as preceding). c. capsule (Steward et al. 502). d. seed (as preceding).

Figure 5. *Hydrangea involucrata*. a. flower (Dorsett & Morse 980). b. capsule (Suzuki December 31, 1948). c. seed (Suzuki December 31, 1948).



5. *Hydrangea aspera* D. Don, Prodrum Florae Nepalensis, 211. 1825.

Shrub or small tree, 1–4 m. tall; branchlets and inflorescence pubescent with stiff and upwardly appressed or curling and erect hairs; leaves variable in shape, lanceolate to ovate, broadly ovate or deltoid, the lanceolate or ovate ones cuneate or rounded at base, 5–35 cm. long, 1.5–15 cm. wide, their length 2.5 to 7 times their width, serrate or serrulate along margin, petioles 0.5–6.5 cm. long, the broadly ovate or deltoid ones rounded or cordate at base, 10–25 cm. long, 7–17 cm. wide, serrate or doubly serrate along margin, petioles 4–21 cm. long; vestiture on lower leaf surface variable and similar to that of stem; inflorescence a flat-topped, many-branched cluster, 10–30 cm. broad; bracts lanceolate, densely hairy on outer surface, glabrous on inner, caducous or remaining; fertile flowers white or blue, numerous, hypanthium 1–1.5 mm. long; sepals 5, 0.4–0.5 mm. long; petals 5, 2–2.5 mm. long, truncate at base, deciduous before stamens; stamens 10, 2–7 mm. long, usually alternately long and short; ovary completely inferior; styles 2, 3 or 4, 0.5–1.5 mm. long; capsules 3–5 mm. long; seeds elliptical, 0.7–0.8 mm. long, 0.3–0.4 mm. wide, tapering at each end into minute tail-like extensions; sterile flowers always present, white, 4-lobed, lobes 1–3.5 cm. long, usually slightly longer than wide, with entire or fimbriate margins. (See plate 6, figure 6.)

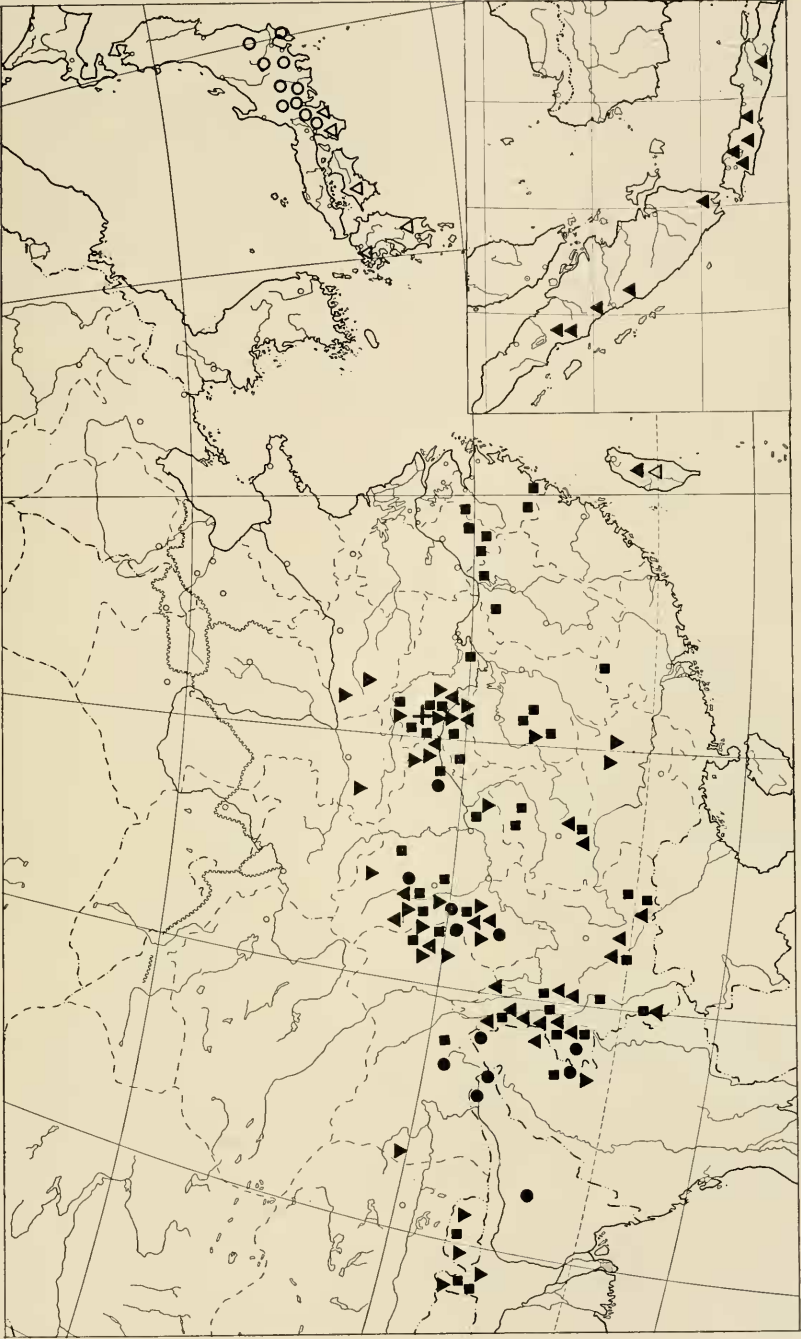
DISTRIBUTION: In woods or thickets, eastern Himalaya Mountains from 1,500 to 2,300 meters; western China from 700 to 4,000 meters; central and eastern China from 250 to 2,100 meters; Formosa, Sumatra and Java from 1,000 to 2,500 meters. (See Map 4.)

KEY TO THE SUBSPECIES OF *HYDRANGEA ASPERA*

1. Stems, lower leaf surface, and petioles strigose or velutinous.
2. Leaves lanceolate or narrowly ovate, their length usually two to five times as great as their width, rounded at base; petioles *usually* 1–5 cm. long.
3. Lower leaf surface strigose, hairs appressed, straight. b. subsp. *strigosa*

MAP 4. Distribution in eastern Asia of
Hydrangea aspera

- subsp. *strigosa*
- ▲ subsp. *aspera* (inset Sumatra and Java)
- ▼ subsp. *robusta*
- ✚ subsp. *Sargentiana*
- subspecies not determined
- △ *Hydrangea sikokiana*
- *Hydrangea involucrata*



3. Lower leaf surface velutinous, hairs erect, somewhat curled, occasionally long coarse pili along midvein, petiole and stem. a. subsp. *aspera*
2. Leaves ovate or broadly ovate, usually less than two times as long as wide, base truncate or cordate; petioles usually 5–17 cm. long. c. subsp. *robusta*
1. Stem, lower leaf surface along midveins, and petioles velutinous, and in addition, interspersed with conspicuous, fleshy trichomes, 2–5 mm. long, split at apex; leaves large, 15 cm. or more long, lower surface velutinous. d. subsp. *Sargentiana*

5a. ***Hydrangea aspera* D. Don subsp. *aspera*.**

Hydrangea aspera D. Don, Prodrum Florae Nepalensis, 211. 1825.

Hydrangea oblongifolia Blume, Bijdragen tot de Flora van Nederlandsch Indië, 920. 1826. Type from Java, *Blume, s. n.* (isotypes W–U, NY).

Hydrangea vestita var. *fimbriata* Wallich, A Numerical List of Dried Specimens of Plants in the East India Company's Museum, published in 1828. Name only. Type from Nepal, *Wallich* in 1821 (K–W, listed in *Wallich's Catalogue* under No. 440).

Hydrangea longipes Hemsley var. *lanceolata* Hemsley, Journal Linnaean Society Botany, 23:274. 1887. Type from Patung, Hupeh, *Henry 1786*. (K, according to Rehder in *Plantae Wilsonianae* 1:40, this is the type.)

Hydrangea aspera var. *strigosior* Diels, Botanische Jahrbücher, 29:375. 1900. Type from Szechuan, *Bock & von Rosthorn 2546* (holotype O).

Hydrangea Kawakamii Hayata, Journal, College of Science, Imperial University, Tokyo, 25(19):90. 1908. Type from Formosa, *Kawakami & Mori 1875* (type not seen, photo CAS).

Hydrangea aspera var. *scabra* Rehder, *Plantae Wilsonianae*, 1:31. 1911. Type from Kangting (Tatsienlu), Sikang, *Wilson 4485* (holotype A).

Hydrangea aspera var. *velutina* Rehder, l. c. 30. Type from Wa-Shan, Szechuan, *Wilson 2405* (holotype A, isotypes K, E).

Hydrangea fulvescens Rehder, l. c. 39. Type from Wushan, Szechuan, *Wilson 1373* (holotype A, isotypes E, K, W).

PLATE 6. Flowers and capsules of some Asiatic species of *Hydrangea*.

Figure 1. *Hydrangea hirta*. a. flower (*Wilson 6958*). b. petal (as preceding). c. capsule (*Wilson 7680*). d. seed (as preceding).

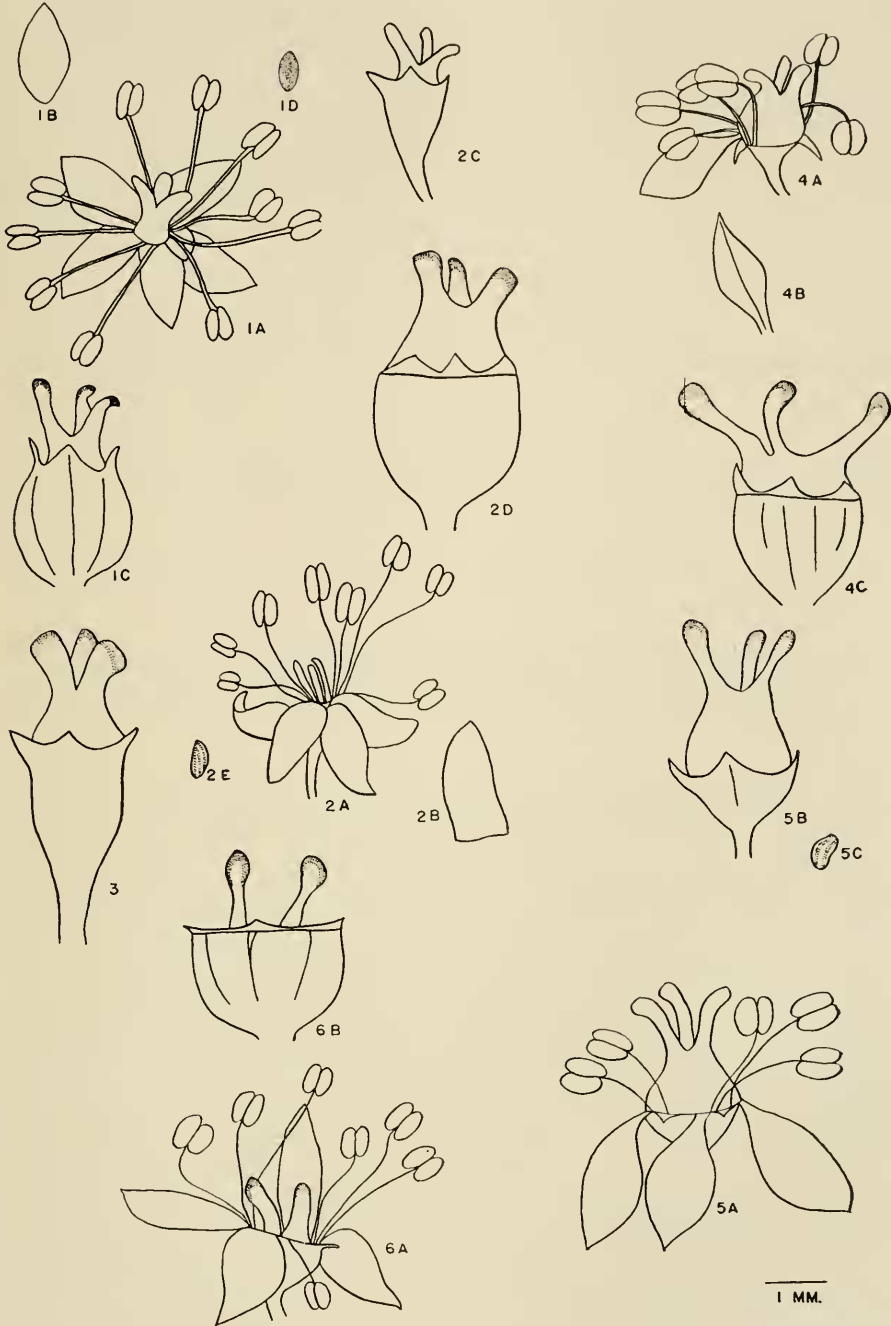
Figure 2. *Hydrangea macrophylla* subsp. *serrata*. a. flower (*Henry M83*). b. petal (as preceding). c. immature capsule (as preceding). d. mature capsule (*Wilson 7621*). e. seed (as preceding).

Figure 3. *Hydrangea macrophylla* subsp. *macrophylla*, immature capsule (*Suzuki July 1917*).

Figure 4. *Hydrangea scandens* subsp. *chinensis*. a. flower (*Tso 21020*). b. petal (as preceding). c. capsule (*Steward & Cheo 1003*).

Figure 5. *Hydrangea scandens* subsp. *liukuensis*. a. flower (*Beattie & Kurihara 10646*). b. capsule (*Wilson 7797*). c. seed (as preceding).

Figure 6. *Hydrangea aspera*. a. flower (*Wilson 2401*). b. capsule (*Wilson 4337*).



- Hydrangea glabripes* Rehder, l. c. 30. Type from Fang Hsien, Hupeh, Wilson 2391 (holotype A, isotypes E, K, W).
- Hydrangea villosa* Rehder, l. c. 29. Type from Wenchuan Hsien, Szechuan, Wilson 1227 (holotype A, isotypes E, K).
- Hydrangea Rehderiana* C. K. Schneider, Handbuch der Laubholzkunde, 2:940, 1912. Type from Nanto, Hupeh, Wilson 1533 (holotype W, isotypes NY, K).
- Premna Merinoi* Lévêillé, Sertum Yunnanense, 3. 1916. Type from "brousses des montagnes à Siai-Ho, 2700 m.", Yunnan, Maire May-July, 1912 (fragment of holotype A).

Leaves lanceolate or narrowly ovate, their length usually two to five times as great as their width, rounded at base; petioles usually 1-5 cm. long; lower leaf surface velutinous, hairs erect, or somewhat curled, occasionally long coarse pili along midvein, petiole and stem. (See plate 2, figure 5.)

TYPE LOCALITY of *Hydrangea aspera*: Narainhetty, Nepal. Type collection: Buchanan September 26, 1802 (holotype BM).

ILLUSTRATIONS:

- H. H. Hu & W. Y. Chun, 1927. *Icones Plantarum Sinicarum*, fasc. I, plate 28.
- New Flora and Silva 7: plate opposite p. 177. 1935, as *H. villosa*.
- B. Hayata, 1908. *Flora Montana Formosae* in Journal, College of Science, Imperial University, Tokyo 25(19), plate 8, as *H. Kawakamii* Hayata.

DISTRIBUTION: CHINA. ANHWEI: Kimen, Wang Shan. CHEKIANG: T'ien-mu Shan, King Yuan, Suian, Yentang Shan, Taishun. HUNAN: Anfu, Sinning, Changning, Sikwangshan district. HUPEH: Changyang, Ch'ing young Hsien, Enshih Hsien, Fang Hsien, Hsing Shan Hsien, He-tan-kon, Ichang, Liang sung you, Peh Yang Tsai, Mo Yu Ping, Nanto, Paokang, Patung, Sui Yeh See, Siao-Ya-tze, Wushan, Wuchang. KIANGSI: Kiu Chi Hsien, Yungshiu. KWANGSI: Pai-yun-an, Ling-chwan district. KWANGTUNG: Lokchong district. KWEICHOW: Kweiting, Pi-tsieh-Hsien, Fan Ching Shan, Tsunyi Hsien, Tungtze. SIKANG: Lushan via Paohing (Mouping), Paohing, Yaan. SZECHUAN: Chung Hsien, Hsi-Chang between Huangnipu and Yaan, Huangnipu, Kwanhsien, Lungan, Nanchuan, Omei Shan, Opian, Wanhsien, Yun-ching Hsien. YUNNAN: Salwin Valley near Champutong, Io chan, Kiao me ti, Ku-long-tschang, Lanping, Lungling, Lu-se, Lichiang, Mengtsz, Po-shang, Pingpien, Shuang-chiang, west flank Shweli-Salwin divide, banks of Shweli River, Shunning, Shang pa, between Tengyueh and Lungling, Weisi, Wenshan. BURMA. Bhamo district near Sinlun Kaba, Kachin Hills. BHUTAN. Tunbje Punakha. INDIA. WEST BENGAL: Darjeeling. SIKKIM: Rumbhi Jhora. TIBET. Tsarong, Ngawchang Valley. SUMATRA. Habin-saran, Seriboe, road from Siantar to Brastagi. FORMOSA. Arisan, Kiraiki.

5b. *Hydrangea aspera* D. Don subsp. *strigosa* (Rehder) McClintock, Journal Arnold Arboretum, 37:373. 1956.

Hydrangea strigosa Rehder, Plantae Wilsonianae, 1:31. 1911.

Hydrangea aspera D. Don var. *macrophylla* Hemsley, Journal Linnaean Society, Botany, 23:273. 1887. Type from "Nanto and mountains to the northward," Hupeh, *Henry s. n.* (K).

Hydrangea aspera D. Don var. *angustifolia* Hemsley, l. c. 273. Type from Ichang, Hupeh, *Henry s. n.* (K).

Hydrangea aspera D. Don var. *typica* Diels, Botanische Jahrbücher, 29:375. 1900. Type from Nanchuan, Szechuan, *Bock & von Rosthorn 299* (holotype O).

Hydrangea aspera D. Don var. *sinica* Diels, l. c. 375. Type from Nanchuan, Szechuan, *Bock & Rosthorn 629* (holotype O).

Hydrangea Hemsleyana Diels var. *lanceolata* (Hemsley) Diels, l. c. 376. (Based on *H. longipes* Hemsley var. *lanceolata* Hemsley.)

Hydrangea aspera D. Don var. *strigosior* Diels, l. c. Type from Wei kuan, Szechuan, *Bock & von Rosthorn 2546* (holotype O).

Hydrangea villosa Rehder var. *Mairei* Léveillé, Catalogue des Plantes du Yunnan, 254. 1917. Type from Kiao me ti, Yunnan, *Maire* July–October 1912 (isotype A).

Hydrangea villosa Rehder forma *sterilis* Rehder, Journal Arnold Arboretum, 11:161. 1930. Type from Changyang, Hupeh, *Wilson 1473a* (holotype A, isotypes K, E, W).

Leaves lanceolate or narrowly ovate, their length usually two to five times as great as their width, rounded at base; petioles usually 1–5 em. long; lower leaf surface strigose, hairs appressed, straight. (See plate 2, figure 4.)

TYPE LOCALITY of *Hydrangea strigosa*: Ichang, Hupeh, China. Type collection: *Wilson 765* (holotype A, isotypes K, US, E, W).

ILLUSTRATIONS:

New Flora and Silva, 9: figure 33, 1937 (habit), as *Hydrangea strigosa* var. *macrophylla*.

Curtis's Botanical Magazine, table 9324, 1933, as *H. strigosa* Rehder.

DISTRIBUTION: CHINA. HUPEH: Changyang, Chienshih, Ichang, On tan tsian. KWANGSI: Tzu Yuen district. KWEICHOW: Kweiting, Lao Shan, Lungli, Pichieh, Pin fa, Pi-tsieh-Hsien, Tating, Touchan. SIKANG: Kang-ting, Lushan via Paohing (Mouping), Ta Kwan. SZECHUAN: Chia-ting, Kwanhsien, Omei Shan, Opien, Tien-Tsian, Wa-Shan, Wenchwan Hsien, Weiknan. YUNNAN: Champutong, Chih-tse-lo, Chungtien on bank of Yangtze, Ku-long-tschang, Liang-shan, Liehiang, Long ky, Lon pon, Lou Lan, Ma ehon, Mengtsz, Paoshan, Pingpien, Siehour-hsien, Shang pa, Tao Shan between Chao and Hungai, Tengyueh, Tehen fong chan, Tsekou, Tsan Shan Range near head of Yangpi Valley, Tunghai, Weisi, between Yangpi and Yungchang-fu, mountains of Yangpi River drainage basin, Yaoan.

BURMA. Hpimaw. NEPAL. Barpak Village, Narainhetty, Thanjei. JAVA. West side of Jang Plateau at Besoeki, Dieng Plateau, Mt. Kendeng, Mt. Malabar, Preanger, Mt. Soembing, Tjibodas on Mt. Gedah. FORMOSA. Mt. Taihei, Mt. Nanko, Nai-taroko.

5c. *Hydrangea aspera* Don subsp. **robusta** (Hooker f. & Thomson) McClintock, Journal Arnold Arboretum, 37: 373. 1956.

Hydrangea robusta Hooker f. & Thomson, Journal Linnaean Society of London, Botany, 2:76. 1858.

Hydrangea robusta var. *Griffithii* C. B. Clarke in J. D. Hooker, Flora of British India, 2:404. 1878. Type from "Eastern Bhotan," *Griffith* 2495 (holotype K, isotype P).

Hydrangea longipes Franchet, Nouvelles Archives, Muséum d'histoire naturelle, Paris, ser. 2, 8:228 (Plantae Davidianae, 2:45). 1885. Type from Paohing (Moupin), Sikang, *David in 1869* (holotype P, isotypes P).

Hydrangea longipes, Hemsley, Journal Linnaean Society of London, Botany, 23:273. 1887. Type from Hupeh, *Henry s. n.* (K).

Hydrangea Rosthornii Diels in Engler's Botanische Jahrbücher für Systematik, 29:375. 1901. Type from Nanchuan, Szechuan, *Bock & von Rosthorn* 471 (isotype W).

Hydrangea Hemsleyana Diels, l. c. 376, based on *Hydrangea longipes* Hemsley, not Franchet.

Hydrangea aspera var. *longipes* (Franchet) Diels, l. c. 374, based on *Hydrangea longipes* Franchet.

Hydrangea Maximowiczii Léveillé, Bulletin Académie international de Géographie Botanique, 12:114. 1903. Syntypes from Kweichow, *Martin & Bodinier* 1654 (E, P), and *Cavalerie* 22 (E).

Leaves ovate or broadly ovate, usually less than two times as long as wide, base truncate or cordate; petioles usually 5–17 cm. long; lower leaf surface strigose, hairs appressed, straight.

TYPE LOCALITY of *Hydrangea robusta*: Sikkim. Type collection: *J. D. Hooker s.n.* (holotype K, isotypes K, NY, BM, C, G, P, W, S).

ILLUSTRATIONS:

H. H. Hu and W. Y. Chun, *Icones Plantarum Sinicarum*, fasc. III, plate 140, as *Hydrangea longipes* Rehder, plate 141, as *Hydrangea Rosthornii* Diels.

DISTRIBUTION: CHINA. HONAN: Lushih, Sunghsien. HUNAN: Anfu. HUPEH: Changlo Hsien, Changyang, Chienshih, Hsing Shan Hsien, Hiang sung you, Ichang, Nanto, Paokang, Patung, Wan Tsao Chan. KANSU: Lower Tebbu country between Hera Sambaku & Dayaya gorge, Wantsang. KWANGSI: Chuen Yuen, Kweilin district, Sankiang Hsien. KWEICHOW: Lao Shan, Tunyun. SHANSI: Locality not stated. SHENSI: Mt. Kin-quan-san, Tai-pei-shan. SIKANG: Kangting, Paohing, Wu Ya Ling. SZECHUAN:

Hungya, Nanchuan, Omei Shan, Opien, Wa-shan, Wenchuan Hsien, Weiknan. YUNNAN: Kiukiang Valley (Taron), Long ky, Shang pa, Tehen fong chan. BURMA. Bhamo. BHUTAN. Mirichoma Timpu, Trashiyangsi. INDIA. UTTAR PRADESH: Garhwal. WEST BENGAL: Darjeeling. SIKKIM: Khursiang, Rhikisun, Sureil. TIBET. Yigrong Valley. FORMOSA. Arisan, Ariko-Banti.

5d. *Hydrangea aspera* Don subsp. *Sargentiana* (Rehder) McClintock, Journal Arnold Arboretum, 37: 373. 1956.

Hydrangea Sargentiana Rehder, Plantae Wilsonianae, 1:29. 1911.

Stem, lower leaf surface along midveins, and petioles velutinous, and in addition, interspersed with conspicuous, fleshy trichomes, 2–5 mm. long, split at apex; leaves broadly ovate, 15 cm. or more long.

TYPE LOCALITY: Hsing Shan Hsien, Hupeh Province, China. Type collection: *Wilson 772* (holotype A).

ILLUSTRATIONS:

H. H. Hu & W. Y. Chun, 1933. *Icones Plantarum Sinicarum*, fasc. III, plate 138.

New Flora and Silva, 12: figure 39, 1940 (habit), and 9: figure 32, 1937 (habit).

Curtis's Botanical Magazine, table 8447. 1912.

DISTRIBUTION: CHINA. HUPEH: Hsing Shan Hsien, Wan Tsao Chan.

DISCUSSION OF *Hydrangea aspera*

Hydrangea aspera is a wide-ranging species, occurring from the eastern Himalayas across western and south-central China and on the islands of Formosa, Sumatra, and Java. It varies throughout this range in size and shape of the leaves and in the pubescence of the lower leaf surface. Most of the names listed in the synonymy were based on such variants.

The leaves vary in shape from lanceolate to ovate, often broadly ovate; their bases are cuneate, rounded or truncate, or occasionally cordate. In actual size they vary in length from 8 cm. to as much as 30 cm. The petiole length varies also, and is often associated with leaf shape. Thus a broadly ovate leaf usually has a longer petiole than one which is lanceolate. The pubescence may be strigose with straight hairs which are appressed and arranged along the veins and veinlets more or less at right angles to them in a regular fashion, or arranged along the veins somewhat irregularly, or the pubescence may be velutinous with curled erect hairs. Although various combinations of leaf shape and vesture occur, most individuals fall into the following categories: 1, leaves lanceolate or ovate, and 2,

leaves ovate; often broadly so. In the first of these categories, the pubescence may be either strigose, referred here to subsp. *strigosa*, or velutinous, referred here to subsp. *aspera*. In the second category, the pubescence is mostly strigose and appressed, referred here to subsp. *robusta*. Most of the herbarium material examined can be referred to these three taxa, but there are some specimens which clearly are intermediate. A fourth group, subsp. *Sargentiana*, has large, broadly ovate leaves, but its chief distinguishing character is the presence of conspicuous, more or less turgid trichomes on the stem, petioles, and lower leaf surface along the midvein.

Don stated in his description of *Hydrangea aspera* that this species was based on a collection made by "Hamilton" at Narainhetty, Nepal. In the British Museum (Natural History) there is a specimen from the Lambert Herbarium collected by "Dr. Buchanan" at Narainhetty, September 26, 1802. It may be considered to be the type of *H. aspera*.

Stapf in discussing the variation of *Hydrangea strigosa* Rehder (Curtis's Botanical Magazine, 156: tab. 9324, 1933) referred to the relation of this taxon to *H. aspera* Don, stating that the two may be given specific rank or be treated as minor groups within *H. aspera* sensu lato (i.e. *H. aspera protonyma* and *H. aspera strigosa*). Stapf clearly stated that he recognized the first alternative. Since Stapf did not accept the category referred to by the name *H. aspera strigosa*, his publication of this combination is not valid according to Article 43 of the International Rules which states that a name is not valid which is not accepted by the author who published it.

Subsection 3. CALYPTRANTHAE

Hydrangea, sect. *Hydrangea*, subsect. *Calyptranthe* (Maximowicz) McClintock, Journal Arnold Arboretum, 37:373. 1956.

Hydrangea, sect. *Calyptranthe* Maximowicz, Mémoires Académie impériale des Sciences de St. Pétersbourg, ser. 7, 10(16):6 (Revisio Hydrangeorum Asiae Orientalis), 1867. Schneider, Handbuch der Laubholzkunde, 1:384, 1905, as subgenus.

Flowers white; petals cohering at apex and falling together as a cap or calyptra; stamens 10, 15 or 20; ovary inferior; capsule truncate at apex; styles free to their bases; seeds with a rounded wing surrounding body of seed. Only one species, *Hydrangea anomala* D. Don, widespread in eastern Asia.

6. *Hydrangea anomala* D. Don, Prodrum Florae Nepalensis, 211. 1825.

Woody climber; branchlets and inflorescence sparsely pubescent with upwardly spreading hairs, 0.5 mm. long; leaves ovate, cuneate, truncate, or cordate at base, acute or acuminate at apex, 6–15 cm. long, 3.5–10.5 cm. wide, their length 1.5 to 2 times their width, glabrous except for scattered

hairs or clumps of hairs along midvein on lower surface; inflorescence a flat-topped, several-branched cluster; involueral bracts lanceolate or ovate-lanceolate, membranous; fertile flowers white; hypanthium 1.5–2 mm. long; calyx lobes 5, 0.5–0.9 mm. long; petals 5, 2–3 mm. long, remaining attached and falling as a cap before the stamens elongate, cap apiculate or rounded at apex; stamens 9–20, 3–5 mm. long, 3 to 4 times as long as styles; ovary inferior; styles 2 or 3, 1–1.3 mm. long; capsule glabrous, 2.5–4.5 mm. long, styles 1–3 mm. long; seeds 1.5–2 mm. long, 1–1.5 mm. wide, nearly round, winged all around; sterile flowers usually present, white, sepals rounded, 1–2 cm. in diameter. (See plate 5, figure 4.)

DISTRIBUTION: Woods and mixed forests in Japan from sea level to 2,000 meters, on Honshu, Kyushu and Hokkaido islands; in Korea on Dagelet and Quelpaert Islands; in the eastern Himalaya Mountains of northern India, from 1,200 to 2,500 meters, and in west central to east central China, from 600 to 3,800 meters. (See Map 5.)

KEY TO THE SUBSPECIES

1. Stamens 9 to 15 subsp. *anomala*
 1. Stamens 15 to 20 subsp. *petiolaris*

6a. *Hydrangea anomala* D. Don subsp. *anomala*.

Hydrangea anomala D. Don, Prodrum Florae Nepalensis, 211. 1825.

Hydrangea altissima Wallich, Tentamen Florae Nepalensis, 2: t. 50. 1826. Type from Nepal, Wallich Catalogue No. 439/1.

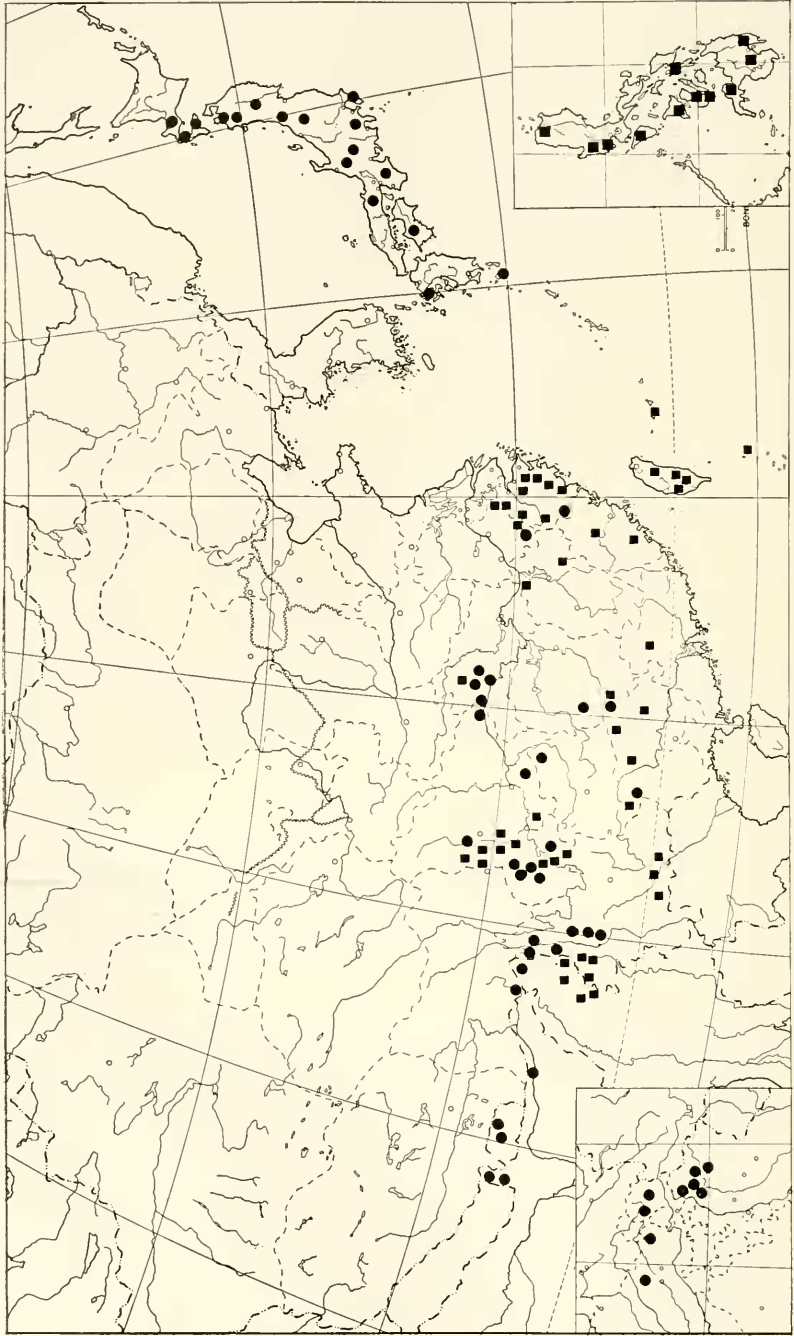
Stamens 9 to 15.

ILLUSTRATIONS:

N. Wallich, Tentamen Florae Nepalensis, 2: t. 50, 1826. As *Hydrangea altissima*.

H. H. Hu & W. Y. Chun, Icones Plantarum Sinicarum, fasc. III, plate 142. 1933.

DISTRIBUTION: Eastern Himalayas and western and central China. CHINA. ANHWEI: Hwang Shan. CHEKIANG: Tihtai Shan; Kingyuan. HUNAN: Yun Shan near Wukang. HUPEH: Hsin Tien-tsze; Paokang; Ichang; Hingshan; Patung. KWANGSI: Ling Wan district; Lucheng; Shan Chuen to Tzeyuan district. KWEICHOW: Fan Ching Shan; Shihtsien district. SZECHUAN: Omei Shan; Nanchwan; Kwanhsien; Wushan; O'Pien Hsien; Ma-pien Hsien; Wa-shan; Tchen-keou-tin. YUNNAN: Tali Range; Mt. Gitsa west of Mekong and north of Weisi; Yungshan; Weisi; Shang-pa; Kungshan (Chamutang, Champutong); Niangonang; Mingkwong Valley; Kani Pass, N. Maikha-Salween divide; Shweli-Salween divide; Ma Nung Mt. near Tali. INDIA. ASSAM: Talung Dzong, Balipara frontier. UTTAR



MAP 5. Distribution in eastern Asia of ● *Hydrangea anomala* (inset western Himalayas) and ■ *Hydrangea scandens* subsp. *chinensis* (inset Philippine Islands).

PRADESH: Dehra Dunn Dist., Deohan; Chakrata; Siwalik and Jaunsar divisions; Chekerli, Siwalik and Jaunsar divisions; Landour; Dhanolti; Garhwal Dist., Tehri Dist. SIKKIM: without definite locality. HIMACHAL PRADESH: Chamba Dist.; Simla district. PUNJAB: Chenab Valley on ascent to Pass Punjab; Kangra Dist.; Nagkanda; Dharmasala; Kulu; Jibhi; Bushire; Manali in Lahul subdivision; Kanugad; Kumaun dist. WEST BENGAL: Darjeeling. NEPAL. Doti; Montes Shandaghery, Sherpore; Sermore; Thare. TIBET-BURMA FRONTIER. Seinghku Wang; Adung Valley; Kangfang route. BHUTAN. Tilageng Punakha; Kadam Punakha; Shambling, Kuru ehu valley; Transmiyangse Dzong.

6b. *Hydrangea anomala* D. Don subsp. *petiolaris* (Siebold & Zuccarini) McClintock, Journal Arnold Arboretum, 37: 373. 1956.

Hydrangea petiolaris Siebold & Zuccarini, Flora Japonica, 1: 108, t. 54. 1839 or 1840.

Hydrangea ? bracteata Siebold & Zuccarini, l. c. 172, t. 92. 1841. No type specimen was designated for this nor the following name. The plates may be considered to represent the types in each case.

Hydrangea cordifolia Siebold & Zuccarini, l. c. 113, t. 59, fig. 2. 1839 or 1840.

Hydrangea scandens Maximowicz. Mémoires Académie impériale des Sciences de St. Pétersbourg, ser. 7, 10(16): 16. 1867. *Non* Seringe 1830, *nec* Poeppig 1830. Based on the above two taxa of Siebold and Zuccarini.

Hydrangea glabra Hayata, Journal College of Science, Imperial University, Tokyo, 25 (art. 19): 89, plate 6. 1908. Type from Formosa, *Kawakami & Mori 1787*. (Type not seen, photo CAS.)

Hydrangea tilaefolia Lévêillé, in Fedde's Repertorium Novarum Specierum 8: 282. 1910. Three syntypes, *Taquet 809* (K, E, G), *Faurie 1654* (E, G, BM), 358 (E, BM), all from Dagelet Island, off the south coast of Korea.

Stamens 15 to 20.

TYPE LOCALITY: Japan. Type specimen: No specimen is mentioned. The plate (*Flora Japonica* 1: t. 54) may, therefore, be considered to represent the type.

ILLUSTRATIONS:

B. Hayata. Flora Montana Formosae in Journal, College of Science, Imperial University, Tokyo, 25 (art. 19): plate 6. 1908. As *Hydrangea glabra* Hayata.

Curtis's Botanical Magazine, plate 6788. 1884. As *H. petiolaris*.

Siebold and Zuccarini. 1839 or 1840. Flora Japonica, 1: t. 59, figure II, as *H. cordifolia*, and t. 54, as *H. petiolaris*.

New Flora and Silva, 1: figure 43, 1929 (habit).

New Flora and Silva, 9: figure 31, 1937 (habit). This, and the above illustration, as *H. petiolaris*.

DISTRIBUTION: SOVIET FEDERATED SOCIALIST REPUBLIC. Sakhalin (Karafuto): Oko. JAPAN. HONSHU ISLAND: Aomori Prefecture: Tanabu; Hakkoda; Mts. of Shichinoki. Osaka Prefecture: Mt. Kongosan. Akita Prefecture: Akita. Gifu Prefecture: Mt. Kasagi; Mitaka. Hyogo Prefecture: Tii-mura; Ashiu. Nagano Prefecture: Otake-gawa; Mt. Izuna; Shinano. Wakayama Prefecture: Sitigawa-mura. Yamagata Prefecture. Nara Prefecture: Tonamine; Mt. Misen. Kanagawa Prefecture: Mt. Hakone. Tochigi Prefecture: Chuzenji; Shiobara. Shizuoka Prefecture: Shojiko; Mt. Amagi on Idzu Peninsula. Iwate & Miyagi border, Mt. Kurikoma. Yamanashi Prefecture: between Fujiyoshida and Lake Shoji. Gumma Prefecture: Mt. Akagisan; Aze. HOKKAIDO ISLAND. Ishikari Subprefecture: Sapporo; Maru-yama. Abashiri Subprefecture: Kitami Fuji. Oshima Subprefecture: Hakodate. Hidacha Subprefecture: Erimo Cape. Iburi Subprefecture: Noboribetsu; Muroran. Shiribeshi Subprefecture: Moribetsu. Soya Subprefecture: Soya Cape (Cape Romanzoff). KYUSHU ISLAND. Kago-shima Prefecture: Yaku-shima. Fukuoka Prefecture: Hikosan. SHIKOKU ISLAND. Kochi Prefecture. FORMOSA. Arisan. KOREA. Dagelet and Quel-paert islands.

DISCUSSION OF *Hydrangea anomala*

Throughout its wide geographical range, *Hydrangea anomala* varies but little. The most obvious variation is in the number of stamens; the Himalayan and Chinese plants have 9 to 15, and the Japanese 15 to 20. The Japanese plants have been considered to be a separate species from the Himalayan and Chinese plants. However, the differences between the two groups do not seem to warrant specific status for them and they are here treated as subspecies.

Don stated in the *Prodromus* that he based *Hydrangea anomala* on a collection made by Wallich in Nepal. Since there was no such specimen in the Lambert Herbarium in the British Museum it was assumed that it must be in the Wallich Herbarium at Kew. In the Wallich Herbarium there are three collections of *H. anomala* written up as follows under Wallich's name for the species in his *Numerical List*:

"439 *Hydrangea altissima* Wall. in Herb. 1824.

1. Napalia 1821
2. Kumaon, R. B.
3. Sermore, Lieut. Gerard."

Although most of the material in the Wallich Herbarium was brought by Wallich to England on his return from India in 1828 some had been sent ahead previous to this date⁴. Material under No. 439 was received

⁴ Wallich so stated this in his explanation of the purpose of his *Numerical List*; see Kew Bulletin for 1913, p. 256.

in England in 1824 and was available to Don before work on the *Prodromus* was completed.

A significant point in Don's description of *Hydrangea anomala* is the statement that the flowers are small and uniform and that there are no sterile flowers. It may have been for this reason that Hooker and Thomson in 1857⁵ placed *H. anomala* in synonymy under *Adamia cyanea*, a species considered today to belong in the genus *Dichroa*. Don's description of *H. anomala* further states that it has two short, thick, recurved styles. While it is true that *Dichroa* has no sterile flowers, it has more than two styles, and these are not short, thick, or recurved.

Of the three specimens of "*Hydrangea altissima*" in the Wallich Herbarium under No. 439, only one, No. 439/1, was collected by Wallich. This specimen consists of a branch bearing two young inflorescences on which sterile flowers are not evident, and a detached portion of an inflorescence which is in anthesis and has sterile flowers. The label reads: "Sheopore. Montes Chandaghery. May 1821." Since the specimen was collected by Wallich in Nepal, and consists of a branch without evident sterile flowers, it presumably was the specimen on which Don based his *H. anomala*. In the material recognized in this paper as *H. anomala* there were several specimens which lacked sterile flowers. The detached inflorescence mentioned above may not have been part of the specimen which Don saw, but may have been added later when the specimen was mounted.

Wallich published *Hydrangea altissima* in the *Tentamen* the year following the publication of Don's *Prodromus*. *H. altissima* was illustrated on plate 50, but no description accompanies this plate and there is no indication of the specimen on which Wallich based his name. The plate of *H. altissima* appears to have been made from a painting in the East India Company's collection in the herbarium at Kew. This, in turn, appears very similar to Wallich's specimen No. 439/1, with the exception of the fact that in the specimen, the flowers are mostly in bud, while the inflorescences shown on the painting have fully opened flowers. It seems conclusive that the specimen in the Wallich Herbarium, 439/1, served first as the basis of Don's *H. anomala*, and later as the material for the painting in the East India Company's collection from which the plate of *H. altissima* in Wallich's *Tentamen* was adopted.

Maximowicz in 1867 cited the three species of Siebold and Zuccarini, listed here as synonyms of *Hydrangea anomala* subsp. *petiolaris*, under his name of *H. scandens*. In his discussion of these species of Siebold and Zuccarini, Maximowicz mentioned particularly *H. bracteata* and the plate representing it in the *Flora Japonica* (vol. 1, table 92). This plate shows a branch, the leaves and bracts of which resemble those of *H. anomala*, but with flowers having 10 stamens and petals which are separated and

⁵ See Journal Linnaean Society Botany, 2:76.

not joined together to fall as a calyptra. Maximowicz pointed out that the Japanese plant of this relationship had 15 and not 10 stamens. He suggested that the illustrator had made a grave error in this illustration and that the error unfortunately was accepted by the describers. This explanation may be as good as any for explaining the anomaly of the plant pictured. The plant is referred here questionably to *H. anomala* subsp. *petiolaris* because of its Japanese origin.

Subsection 4, PETALANTHE

Hydrangea, sect. *Euhdrangea*, subsect. *Petalanthe* (Maximowicz) Rehder, *Plantae Wilsonianae*, 1:37. 1911.

Hydrangea, sect. 1, *Euhdrangea*, ser. 1, *Petalanthe*, *Japonico-sinuensis* Maximowicz, *Mémoires Académie imperiale des Sciences de St. Pétersbourg*, ser. 7, 10 (16):6 (Revisio *Hydrangearum Asiae Orientalis*). 1867. In part.

Flowers white or blue; ovary half superior; capsule conical at apex; styles longer than conical disk; seeds not caudate. Chinese and Japanese species.

TYPE SPECIES: *Hydrangea hirta* Siebold & Zuccarini.

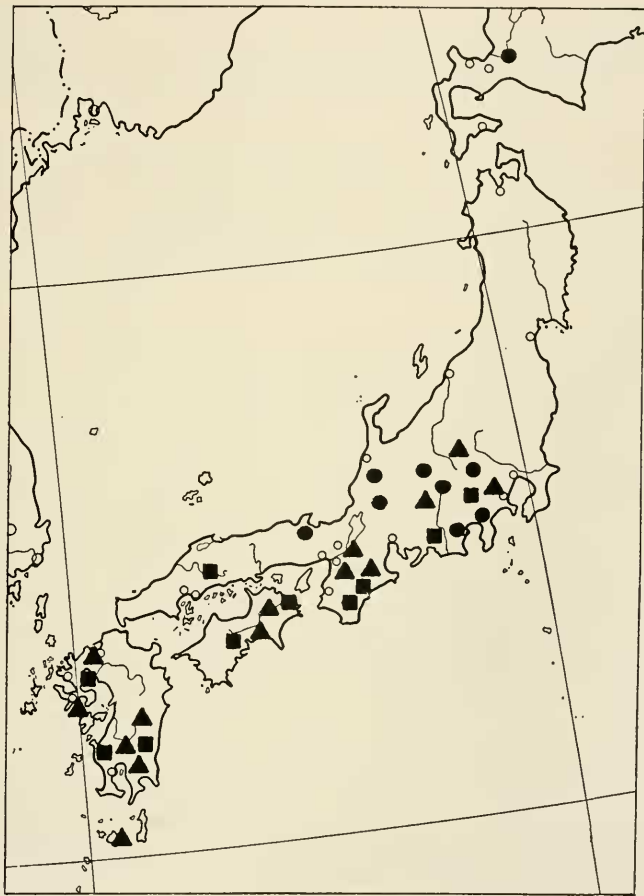
7. *Hydrangea hirta* (Thunberg) Siebold, *Flora*, 11:757. 1828.

Viburnum hirtum Thunberg, *Flora Japonica*, 124. 1784.

Shrub, 0.5–2 m. tall, branchlets and inflorescence pubescent with coarse, upwardly appressed hairs, 0.4–1 mm. long, and in addition, longer spreading hairs on branchlets; leaves 3–10.5 cm. long, 2.5–7 cm. wide, length equaling width to as much as 2.5 times as great, oval, deeply serrate, with serrations 3–8 mm. deep, both surfaces with scattered appressed hairs along veins and veinlets; petiole 1–3.5 cm. long, pubescent with spreading hairs; inflorescence a rounded, compound cluster, 2–10 cm. wide; bracts 1 or 2 pairs below inflorescence, 1–3 cm. long, leaf-like, lanceolate, entire or with 2 to 4 deep serrations; fertile flowers only present, bluish; hypanthium 0.5–1 mm. long; calyx lobes 5, rarely 4, 0.5 mm. long; petals 5, rarely 4, 1.5–2 mm. long, reflexed before falling, cuneate at base; stamens 10, rarely 8, 2.5–4 mm. long, 2 to 3 times as long as styles; ovary half superior; styles 3 or 4, 1–1.5 mm. long, united for 0.3–0.5 mm., free for 0.6–1 mm.; capsule 3–3.5 mm. long (including styles); hypanthium 1.5–2 mm. long, styles 1–2 mm. long, united for 0.5–1 mm., less than one-half of their length; seeds 0.7–0.9 mm. long, 0.4–0.5 mm. wide, elliptical, blunt at each end. (See plate 6, figure 1.)

TYPE LOCALITY: Japan. Type collection: *Thunberg* (holotype UPS, photo A).

DISTRIBUTION: Mixed forests and woods, on Honshu Island in Japan, on Okinawa Island in the Ryukyu Islands, from 200 to 1000 meters. JAPAN. HONSHU ISLAND: Kyoto Prefecture: Atago County; Kyoto. Saitama Prefecture: Mitsumine; Chiehibu; Mt. Takamidzu. Kanagawa Prefecture: Hakone Mts.; Hanno; Mt. Takao. Shizuoka Prefecture: Shiojiko (Fujiyama region); Shimoda. Nagano Prefecture: Mt. Asama; Atago near Karuizawa; Gora to Miyanoshita; Kiso near Ontake-san. Tochigi Prefecture: Nikko; Chuzenji. Tokyo Prefecture: Mt. Takao; Mt. Sougakuzan. Gifu Prefecture: Hokenomura; Nakayama-hichiri. Hyogo Prefecture:



MAP 6. Distribution in Japan of

● *Hydrangea hirta*

▲ *Hydrangea scandens* subsp. *scandens*

■ *Hydrangea scandens* subsp. *liukiuensis*

Rokkasan; Kobe. Yamanashi Prefecture: Nishi-yatsushiro. Wakayama Prefecture: Nachi. Nara Prefecture: Mt. Omine. RYUKYU ISLANDS. Okinawa Island: Kunigawa County. (See Map 6.)

DISCUSSION: *Hydrangea hirta* is the only one of the Asiatic species of *Hydrangea* which normally does not have sterile flowers. Its leaves have a characteristic shape, which gives them a "nettle-like" appearance. These two characters, lack of sterile flowers and "nettle-like" appearance of the leaves, distinguish this species from *H. scandens* which it resembles most closely in structure of flowers and fruits. Its geographical range is restricted to the island of Honshu in Japan, and Okinawa Island.

Hydrangea amagiana Makino (Journal of Japanese Botany 8: 31, 1932) is considered by Makino to represent a possible hybrid between *H. hirta* and *H. scandens* subsp. *scandens*. It is described as having coarsely serrate-dentate leaves, no sterile flowers, and petals cuneate at base. The specimen which was the basis for Makino's species came from Izu Peninsula, Honshu Island. A similar plant grows in Nippara, Musashi province, according to Hiyama (see Journal of Japanese Botany 10: 391, 1943). The writer has seen neither of these specimens and therefore cannot evaluate *H. amagiana*.

8. ***Hydrangea scandens*** (L. f.) Seringe in DeCandolle, Prodrumus, 4: 15. 1830. *Non* Poeppig, 1830, *nec* Maximowicz, 1867.

Shrub or small tree, 1 to 4, or rarely, as much as 6 meters tall; branchlets and inflorescence pubescent with upwardly appressed hairs, varying in amount from sparse, with hairs 0.1–0.5 mm. long, to more dense with longer hairs, 1–2 mm. long, spreading or appressed, rarely nearly glabrous; leaves ovate, 2–18.5 cm. long, 1–8 cm. wide, 1.5 to 4 times as long as wide, glabrous to pubescent in vicinity of veins, petiole 1–3 cm. long, pubescent as branchlets; inflorescence a branched, compound, flat-topped cluster, 2–18 cm. broad, terminal or axillary, involueral bracts none; fertile flowers yellow or blue, few or numerous; hypanthium 0.5–1.5 mm. long; calyx lobes 5, 0.3–3.2 mm. long; petals 5, 1.2–4.5 mm. long, cuneate at base, reflexed, falling with stamens; stamens 10, 1.2–5.5 mm. long, slightly shorter than styles to as much as twice their length; ovary half superior; styles usually 3, occasionally 2, 4, or 5, 1.3–3.5 mm. long, united for 0.5–1.5 mm., $\frac{1}{3}$ to $\frac{2}{3}$ of their length, free portion 0.5–2 mm. long; capsules 3–8.5 mm. long (including styles), styles 1.5–5.5 mm., united for 0.8–3 mm., less than half their length, free portion 0.7–2.5 mm.; seeds 0.5–0.7 mm. long, 0.3–0.7 mm. wide, oval, blunt at each end; sterile flowers present; sepals (yellow or) white or blue, turning red or yellow in age, 1–3 cm. long, nearly as broad as long, margins serrate, apex acute or rounded. (See plate 6, figures 4 and 5.)

DISTRIBUTION: Western to southwestern China, Formosa, the Philippine Islands, Japan, and the Ryukyu Islands. (See Maps 5 and 6.)

KEY TO THE SUBSPECIES OF *HYDRANGEA SCANDENS*

1. Shrubs or small trees up to 4, or even 6 m. tall; inflorescences usually terminal; fertile flowers usually numerous.
2. Stems and leaves pubescent with short upwardly curled hairs or glabrous. c. subsp. *chinensis*
2. Stems and leaves hirsute pilose. d. subsp. *kwangtungensis*
1. Small shrubs, usually less than 2 m. tall; inflorescences usually axillary; fertile flowers usually few (10 to 15) in number.
3. Leaves 3.5-9 cm. long, 1-3 cm. wide; bark grayish-brown or tan, dull in appearance. a. subsp. *scandens*
3. Leaves 2-5 cm. long, 1-2 cm. wide, sometimes with white band along midvein; bark reddish-brown, having a somewhat polished appearance. b. subsp. *liukiensis*

8a. *Hydrangea scandens* (L. f.) Seringe subsp. *scandens*.

Viburnum scandens L. f., Supplementum, 184. 1781.

Viburnum virens Thunberg, Flora Japonica, 123. 1784.

Hydrangea virens (Thunberg) Siebold, Nova Acta: Academia (caesarea) Leopoldino-Carolina, 14:690. 1829.

Hydrangea scandens (L. f.) Seringe in DeCandolle, Prodrumus, 4:15. 1830.

Leaves 3.5-9 cm. long, 1-3 cm. wide, green, upper surface dull, bark grayish brown or tan, dull in appearance.

TYPE LOCALITY: Japan. Type collection: A specimen labeled *Viburnum scandens* in the J. E. Smith collection of the Linnaean Herbarium in London is the type of *Viburnum scandens* L. f.

DISTRIBUTION: JAPAN. HONSHU ISLAND: Gifu Prefecture: no locality. Hyogo Prefecture: Nunobiki, Rokkosan. Kanagawa Prefecture: Miyano-shita, Ojigoku, Ohadzu to Hakone, Yokohama, Tonosawa, Hakone. Nara Prefecture: Nara, Mt. Odaigahara, Yoshino. Saitama Prefecture: Mt. Idzugatake, Mt. Takao, Mitsumine-san, Chichibu, Ome. Shizuoka Prefecture: Atami, Fujiyama, Mt. Amagi on Izu Peninsula, Suruga. Tokyo Prefecture: Nishi-tama-gun, Takao-yama. Wakayama Prefecture: Shingu, Mt. Nachi. Yamanashi Prefecture: Mt. Minobu. KYUSHU ISLAND: Fukuoka Prefecture: Mt. Kosho. Kagoshima Prefecture: Enoo, Yakushima, Mt. Kirishima, Mt. Takakuma, Kagoshima. Kumamoto Prefecture: Amakusa Island. Miyazaki Prefecture: Sobo-san, Minaminaka-gun. Nagasaki Prefecture: Mt. Fugen, Nagasaki. SHIKOKU ISLAND. Tokushima Prefecture: no locality. Kochi Prefecture: Shimonanokama. FORMOSA. Bankinsing.

8b. *Hydrangea scandens* (L. f.) Seringe subsp. *liukiensis* (Nakai) McClintock, Journal Arnold Arboretum, 37:373. 1956.

Hydrangea liukiensis Nakai, Botanical Magazine, Tokyo, 25:63. 1911.

Hydrangea luteo-venosa Koidzumi, Botanical Magazine, Tokyo, 39:4. 1925. (No type specimen was designated.)

Leaves 2–5 cm. long, 1–2 cm. wide, variegated with a yellow band along midvein and secondary veins, upper surface lustrous, lower usually glaucous, bark reddish-brown, with more or less polished appearance. (See plate 6, figure 5.)

TYPE LOCALITY of *Hydrangea liukiensis*: Ryukyu Islands. Okinawa, Nogodake. Type collection: *Tanaka 187* (photo CAS). Specimen not seen by the writer.

DISTRIBUTION: JAPAN. HONSHU ISLAND. Hiroshima Prefecture: Onomichi. Hyoga Prefecture: Mt. Maya, vicinity of Kobe, Rokkosan. Shizuoka Prefecture: Atami, Amagisan, Shimoda, Shuzenji. Wakayama Prefecture: Mt. Naehi, Koyasan, Yahazuyama. KYUSHU ISLAND. Kagoshima Prefecture: Makizono. Miyazaki Prefecture: Kitagomura. Nagasaki Prefecture: Nagasaki. Kumamoto Prefecture: Amakusa Island. SHIKOKU ISLAND. Mts. of Kochi, Mts. of Iyo. Kochi Prefecture: Nishinokawa, Yasuda. RYUKYU ISLANDS. Okinawa Island, Kunigami.

DISCUSSION: *Hydrangea scandens* subsp. *liukiensis* is characterized by its small leaves, which often have a yellow band along their midveins, and the reddish-brown stems. It is distinguished from *H. scandens* subsp. *scandens*, which also occurs in Japan, by these characters.

Hydrangea luteo-venosa Koidzumi was described as having small leaves (to 4 cm. long) which have yellow-white veins and an inflorescence consisting of about 20 flowers. The author apparently based it on Asa Gray's interpretation of the Williams and Morrow specimen collected at Simoda on the Perry Expedition and which Gray determined as *H. virens*.

8c. ***Hydrangea scandens*** (L. f.) Seringe subsp. ***chinensis*** (Maximowicz) McClintock, Journal Arnold Arboretum, 37:373. 1956.

Hydrangea chinensis Maximowicz, Mémoires Académie impériale des Sciences de St. Pétersbourg, ser. 7, 10(16):7. 1867.

Hydrangea Lobbii Maximowicz, l. c. 15. Type from Philippine Islands, *Lobb 446* (isotypes K, E, BM, W, G).

Hydrangea Davidii Franchet, Nouvelles Archives Muséum d'histoire naturelle, Paris, ser. 2, 8:227. 1885. Type from Paohing (Moupin), Sikang, *David in 1869* (holotype and isotypes P).

Hydrangea Pottingeri Prain, Journal Asiatic Society of Bengal, 67:290. 1898. Type from Kachin Hills, Burma, *Pottinger, May 4, 1897* (holotype K).

Hydrangea Arbostiana Léveillé, Bulletin, Académie internationale de Géographie Botanique, 12:115. 1903. Type from Mont du Collège, Kweichow, *Bodinier 1694* (holotype E, fragment and photo of holotype A, isotypes P, E).

- Hydrangea subintegra* Merrill, Philippine Journal of Science, Botany, 3:408. 1908. Type from Batan Island, Philippine Islands, *Félix, June 1907* (isotypes US, K).
- Hydrangea umbellata* Rehder in Plantae Wilsonianae, 1:25. 1911. Type from Kuling, Kiangsi, *Wilson 1605* (holotype A, isotypes E, US).
- Hydrangea yunnanensis* Rehder, l. c. 37. Two syntypes cited, both from Mengtze, Yunnan, *Henry 10236* (A, NY, K), and *10236B* (K, E, S, A, NY).
- Hydrangea glabrifolia* Hayata, Icones Plantarum Formosanarum, 3:106. 1913. Type from Tandaisan, Formosa, *Mori, April 1910* (specimen not seen, photo CAS).
- Hydrangea macrosepala* Hayata, l. c. 108. Type from Kokei, Formosa, *Nagasaki, April 1903* (specimen not seen, photo CAS).
- Hydrangea obovatifolia* Hayata, l. c. 109. Type from Terasasan, Formosa, *Hayata & Sasaki, July 5, 1912* (specimen not seen, photo US).
- Hydrangea angustipetala* Hayata, Journal College of Science, Imperial University, Tokyo, 30(1):107. 1911. Type from Giran, Formosa, *Kawakami & Mori 1383* (specimen not seen, photo CAS).
- Hydrangea angustifolia* Hayata, Icones Plantarum Formosanarum, 1: plate 32. 1911. No description, plate only, which represents the type.
- Hydrangea angustisepala* Hayata, l. c. 2:4. 1912. Type stated to be from Formosa but no specimen was cited. However, the English description is based on the Latin description of *H. angustipetala*.
- Hydrangea Davidii* Franchet var. *Arbostiana* Lévillé, Flora Kouy-Tcheou, p. 387. 1914. (Presumably based on *H. Arbostiana* Lévillé. Publication has not been seen by the author.)
- Hydrangea pubiramea* Merrill, Philippine Journal of Science, Botany, 12:267. 1917. Type from Tayabas Province, Luzon Island, Philippine Islands, *Ramos & Edaño* herb. no. 26521 (isotypes A, K, US).
- Hydrangea pubiramea* var. *parvifolia* Merrill, l. c. 268. Type from Nueva Ecija Province, Luzon Island, Philippine Islands, *Ramos & Edaño* herb. no. 26511 (isotype US).
- Hydrangea Kawagoeana* Koidzumi, Botanical Magazine, Tokyo, 32:138. 1918. Two syntypes are cited, both from the Ryukyu Islands: Nakanoshima, *Kawagoe 60*, and Takarashima, *Ushiro, May 4, 1917*. (Neither specimen seen, photo of *Kawagoe 60*, CAS.)
- Hydrangea subferruginea* W. W. Smith, Notes from the Royal Botanic Garden, Edinburgh, 11:212. 1919. Type from Htawgaw Valley, Burma, *Ward 1542* (holotype E).
- Hydrangea chloroleuca* Diels, Notizblatt des Botanischen Gartens und Museums, Berlin-Dahlem, 9:1027-1028. 1926. Type from Yungshing Hsien, Kiangsi Province, China, *Hu 799* (isotype A).
- Hydrangea yayeyamensis* Koidzumi, Botanical Magazine, Tokyo, 43:394. 1929. *Oldham 110* ("pro parte") is the only specimen cited. This specimen, cited previously as a syntype of *H. chinensis* by Maximowicz, was the basis of *H. yayeyamensis*, which was considered by Koidzumi to be a Formosan species. *H. chinensis* was emended by Koidzumi to include only Chinese plants.
- Hydrangea formosana* Koidzumi, l. c. Five syntypes, all from Formosa, were cited: *Oldham 110* "partim" (E, K, P, W, S, A, NY), *Ford in 1884* (K), and 3 specimens collected by Price (K).

Hydrangea grossiserrata Engler in Engler & Prantl, *Natürlichen Pflanzenfamilien*, ed. 2, 18a:207. 1930. Type from Yakushima, *Faurie 3934* (isotype G).

Hydrangea stenophylla Merrill & Chun, *Sunyatsenia*, 1:58. 1930. Type from Lok-chong, Kwangtung, *Tso 20617* (NY).

Shrubs or small trees, 1 to 4, or rarely, as much as 6 meters tall; leaves 5–18.5 cm. long, 1.5–8 cm. wide, 1.5 to 4 times as long as wide; inflorescences usually terminal; fertile flowers usually numerous; calyx lobes 0.5–3.2 cm. long; capsules 3–8.5 cm. long.

TYPE LOCALITY: Formosa. Tamsui. Type collection of *Hydrangea chinensis* Maximowicz, lectotype, *Oldham 110* (NY), other specimens of this collection, E, K, P, W, S, A. A syntype of *H. chinensis* Maximowicz is *Fortune A42*, Chekiang in 1845 (K, G, P, W).

DISTRIBUTION: Mixed forests and thickets; on Formosa from sea level to 2,500 meters, the Philippine Islands from 700 to 2,500 meters, and from western to southeastern China from 500 to 3,000 meters. (See plate 6, figure 4.) CHINA. ANHWEI: Hwang Shan, Chuhuashan, Tien Chu Shan. CHEKIANG: Mogan Shan, Ping yan, Suian, T'ien-tai Shan, T'ien-mu Shan, Tihtai Shan, Tsingtien, Changhua, Fenghwa, Hangechow, Kewkiang. FUKIEN: Amoy, Ku-dien, Nanping. HUPEH: Paohang. KIANGSI: Tung-huashan, Kuling, Lu Shan, Yung shing hsien. KWANGSI: Lingehwan district, Yao Shan, Ling Wang Shan, Chuen Yuen, Yeo Mar Shan, Hang-on-yuen. KWANGTUNG: Lokchong, Tsungfa district, Yao Shan, Yuyuen, Tsing Wan Shan, Kweiyang, Lin fa Shan, Nam Shan, Yam na Shan, Sam Kok Shan, Hong Kong. KWEICHOW: Kouy-yang, Fan Ching Shan, between Tjiaulou and Baling, near Dayung, Yao ren shan, Pin fa. SIKANG: Kangting (Tatsienlu), Hanyuan, Hweili, Paohing (Muping), Tienchuan. SZE-CHUAN: Loshan, He-chang Hsien, Opian, Wa shan, Tahsiangling, Tetsehang in valley Kientschang. YUNNAN: Pingpien, Shunning, Shweli-Salween divide, Tengyueh, Yiliang, headwaters of Shweli River, Salween Valley, Pan pien hsien, Yungshan, Wenshan, Tongtchouan, Shangpa, Kiu-kiang Valley, Mengtze, Ningpo, Tschen Fong chan, Kiao Kia, Gan chonen. BURMA. Kachin Hills, Myitkyina, Kangfang, Kambaiti, Htawgaw, Hpi-maw valley, Maikha-Salween divide. PHILIPPINE ISLANDS. BATAN ISLAND: Mt. Iraya, Santo Domingo de Basco. LEYTE ISLAND: No locality. LUZON ISLAND: *Mountain Province*: Benguet Subprovince, Baguio, Mt. Santo Tomas, Mt. Simacoco, Mt. Pulog, Mt. Pauai, Apayao Subprovince, Bayag, Bontoc Subprovince. *Tayabas Province*: Mt. Dingalan. *Nueva Ecija Province*: Mt. Umingan. *Rizal Province*: Balacbac, Montalban, Monte Batay. *Bataan Province*: Mt. Mariveles. MINDANAO ISLAND. *Bukidnon Province*: Mt. Dumalupihan. *Davao Province*: Mt. McKinley, Mt. Mayo. *Cotabato Province*: Mt. Apo. *Misamis Occidental Province*: Mt. Malindang. MINDORO ISLAND. Mt. Haleon. NEGROS ISLAND. *Negros Oriental Province*:

Dumaguete, Cuernos de Negros, Canlaon Volcano. PANAY ISLAND. *Capiz Province*: Mt. Madiass, Mt. Macosolon. FORMOSA. Arisan, Bankinsing, Bukiko, Lake Candidius, Chippon-goe in Taitocho, Daksui Valley near Togun, Hassen-zan, Hori, Hokuto, Kapulan, Kelung, Kiirun, Koarong, Siutiam near Banka, Shirisi near Taihoku, South Cape, Sozan, Taipeh, Mt. Chiehseizan, Dakushu, Taihoku, Tomita, Taiheizan, Taitum, Urai, Tamsui. RYUKYU ISLANDS. CLEOPATRA ISLAND. IRIOMOTE ISLAND, Nakara River region, Urauchi River, Hidori River. OKINOERABU ISLAND. AKUSEKI ISLAND. ISHIGAKI ISLAND, between Maezato Yama and peak south of Omato Yama, Omoto-dake. JAPAN. YAKUSHIMA ISLAND.

DISCUSSION: *Hydrangea scandens* subsp. *chinensis* occurs throughout the range of the species with the exception of Japan. It is distinguished from *H. scandens* subsp. *scandens*, which occurs in Japan, by its generally larger leaves which appear to be stiff and leathery in comparison with those of subsp. *scandens*, the somewhat larger size of its individual plants and its usually terminal inflorescences. These differences are usually sufficient to distinguish the two taxa; however, occasional individuals occur in which these differences are not pronounced.

Throughout its range *Hydrangea scandens* subsp. *chinensis* varies in leaf shape and size. Leaves on the Chinese plants usually are from 5.5–15 cm. in length, and 2–6 cm. in width, their length being 2 to 3.5 times as great as their width, and the pubescence is usually in the vicinity of the midrib and on the petiole. However, there occasionally are found plants with more narrow leaves, ranging from 1.5 to 3.5 cm. in width and which are always glabrous. Such a plant is *Tso 20617*, which is the type of *H. stenophylla* Merrill & Chun. In the Philippine plants, the leaves are somewhat larger, being up to 18.5 cm. long, and 8 cm. wide, while in the Formosan plants the leaves tend to be smaller, being up to 10.5 cm. long and 4 cm. wide.

In addition to the leaf variation in *Hydrangea scandens* subsp. *chinensis*, there is some variation in the length of the stamens and their relation to the length of the style, and in the size of the capsules. In the Chinese plants, the stamens are very slightly longer than the styles, to as much as two times as long; the over-all length of the stamens, the greatest for the entire species, is from 1.5 to 5.2 mm., while the length of the styles is not over 3.5 mm. In both the Formosan and the Philippine plants the stamens are equal in length to that of the styles to about one and one-half times their length. In actual measurement the length of the stamens in the Philippine and Formosan plants is about the same, 1.2–4 mm., but in the Philippine plants the styles are somewhat longer (1.8–3.5 mm.) than those of the Formosan (1.5–2.5 mm.). The largest capsules (from 3.5 to 8.5 mm. long) are found in the narrow-leaved Chinese plants, while for

the Formosan and the broader-leaved Chinese plants the capsules are from 3 to 5.5 mm. long. In the Philippine plants, the capsules are from 5-7.5 mm. long.

From the collector's notes occasionally given on the labels there is seen to be a variation in flower color. Both kinds of flowers may be either white (or ? yellow) or blue, and occasionally the sterile flowers are absent.

Under *Hydrangea chinensis*, Maximowicz cited four syntypes, three from China and one from Formosa. The Formosan collection was made by Oldham (No. 110) in 1864 at Tamsui; duplicates of it are available in several herbaria. The specimen in the herbarium of the New York Botanical Garden has been selected as the lectotype. The other syntypes cited by Maximowicz are: *Fortune 442*, collected in 1845 at Amoy, Chekiang Province, and specimens collected by Bunge and Senjavin (both cited by Maximowicz as being in Herb. Fischer of the Botanic Garden in St. Petersburg), which were not available to the writer. There is some doubt as to whether the Bunge specimen should be identified with *Hydrangea scandens* subsp. *chinensis*. Bretschneider (1898) stated that Bunge, who accompanied the 11th Ecclesiastical Mission of the Russian Government to Peking, in 1830, made collections in the vicinity of this city. *H. scandens* subsp. *chinensis* does not occur in China this far north. The specimen may be *H. heteromalla* which occurs in the vicinity of Peking. The Seniavin (or Senjavin) specimen is mentioned by Bretschneider (1898, vol. 1, p. 620) as belonging to a collection of Chinese plants said to have been received by Dr. Fischer from Seniavin "who from 1838 to 1851 was Director of the Asiatic Department in the Foreign Office." This collection was not made by Seniavin but came to him through the Russian Ecclesiastical Mission at Peking, through whose agency it probably was made in Fukien province. Since Fukien is within the range of *H. scandens* subsp. *chinensis* the specimen may belong to this subspecies.

Maximowicz based his *Hydrangea Lobbii* on a collection by Lobb (No. 446) and said to have been collected in Java. However, according to Merrill (in Philippine Journal of Science, Sect. C, Botany, 10:185, 1915), "the Kew specimen of this collection is labelled Luzon, and this certainly is correct, as the species is common and widely distributed in the mountains of the northern Philippines."

8d. ***Hydrangea scandens* (L. f.) Seringe subsp. *kwangtungensis* (Merrill) McClintock**, Journal Arnold Arboretum, 37:373. 1956.

Hydrangea kwangtungensis Merrill, Journal Arnold Arboretum, 8:7. 1927.

Shrubs 3 to 5 ft. tall; stems, branchlets, and leaves softly villous with hairs 0.5 mm. long; leaves 8-10 cm. long, 3-4 cm. wide, 2.5 times as long as wide; fertile flowers numerous; calyx lobes 1 mm. long; hypanthium 0.5 mm. long; petals 2.2 mm. long; stamens 1.7-2.2 mm. long; 3 or 4

styles, 1.5 mm. long, free portion 1 mm. long; capsules 4.3 mm. long, villous; hypanthium 1.8 mm. long; styles 2.5 mm. long, free portions 1 mm. long, united portion 1.5 mm. long.

TYPE LOCALITY of *Hydrangea kwangtungensis*: China, Kwangtung Province. Type collection: *Peng et al. May 22, 1924*, Canton Christian College herb. No. 12017, collected on the National Geographic Society Expedition under the direction of F. W. Wulsin, (holotype US, isotypes A, UC, W, E).

DISTRIBUTION: CHINA. KWANGTUNG PROVINCE: Lung T'au Mountain near Lu, Tai Mo Shan, Tapu District.

DISCUSSION: *Hydrangea scandens* subsp. *kwangtungensis* is distinguished by the softly villous hairs on its stems and leaves. Its flower and fruit structures are not different from those of the other subspecies of *H. scandens*. Only two collections of this subspecies were seen, both from Kwangtung Province, indicating that its distribution is doubtless restricted.

Subsection 5. HETEROMALLAE

Hydrangea, sect. *Euhdrangea*, subsect. *Heteromallae* Rehder, *Plantae Wilsonianae*, 1:37, 1911.

Hydrangea, section 1. *Euhdrangea*, series 2. *Piptopetalae* Maximowicz, *Mémoires Académie impériale des Sciences de St. Pétersbourg*, ser. 7, 10(16):8. 1867. In part.

Hydrangea, subgenus *Euhdrangea*, section *Japonico-sinensis*, subsection *Piptopetalae* (Maximowicz) Schneider, *Handbuch der Laubholzkunde*, 1:388. 1905. In part.

Flowers white; filaments flattened toward their bases; ovary half superior; capsule conical at apex; styles shorter than conical disk; seeds caudate. Chinese and Japanese species.

9. *Hydrangea paniculata* Siebold, *Nova Acta: Academia (caesarea) Leopoldino-Carolina*, 14: 691. 1829.

Hydrangea Kamienskii Léveillé, *Bulletin, Académie internationale de Géographie Botanique*, 12:115. 1903. Syntypes from Kweichow: *Bodinier 1661* (P, E), and *Martin & Bodinier 1661 bis* (P).

Hydrangea sachalinensis Léveillé, in *Fedde's Repertorium Novarum Specierum*, 8:282. 1910. Type from Sakhalin, *Faurie 439* (holotype E, isotypes A, P, BM, W).

Hydrangea Schindleri Engler, in *Engler & Prantl, Natürlichen Pflanzenfamilien*, ed. 2, 18a:203. 1930. In part. Lectotype from Kuling, Kiangsi, *Schindler 324* (E, K, BM, G, W).

Much branched shrub or small tree, 0.5–7 m. tall; branchlets and inflorescence pubescent with upwardly appressed hairs 0.3–0.5 mm. long;

leaves opposite or ternate, ovate, 7–15 cm. long, 3–10 cm. wide, 1.5 to 2.5 times as long as wide, both surfaces with scattered hairs along veins and veinlets; petiole 1–2.4 cm. long; inflorescence a compound, much branched, pyramidal cluster, 7–25 cm. long, lowermost branches of inflorescence opening first; bracts numerous, linear to ovate, chartaceous, 1–10 mm. long, 0.2–2.5 mm. wide, subtending main branches of inflorescence, reduced upward, few pili on back and along margins; fertile flowers white, very numerous; hypanthium 0.8–1 mm. long, glabrous or with few scattered hairs; calyx lobes 5, 0.5–1 mm. long; petals 5, 2–3 mm. long, ovate, reflexed before falling; stamens 10, 1.7–4.8 mm. long, filaments gradually broadening toward base; ovary half superior; styles 2, 3, or 4, 1.5–2 mm. long, united at base for 0.5–1.5 mm., free for 0.5 to 1.2 mm.; capsule 3.5–5 mm. long, hypanthium 1.5–3 mm. long, styles 2–3.5 mm. long, united for 1.3 to 2 mm., about $\frac{1}{2}$ to $\frac{3}{4}$ of their length; seeds 1.7–3 mm. long, 0.4–0.5 mm. wide, linear, tapering at each end into minute tail-like extensions; sterile flowers always present, white, 4-lobed, lobes ovate, 1.2–2 cm. long, 0.8–1.5 cm. wide. (See plate 5, figure 3.)

TYPE LOCALITY: Japan. Type collection: the specimens collected in Japan by von Siebold are in the Rijksherbarium in Leiden. Presumably the type of *H. paniculata* is there, but the writer has not seen it.

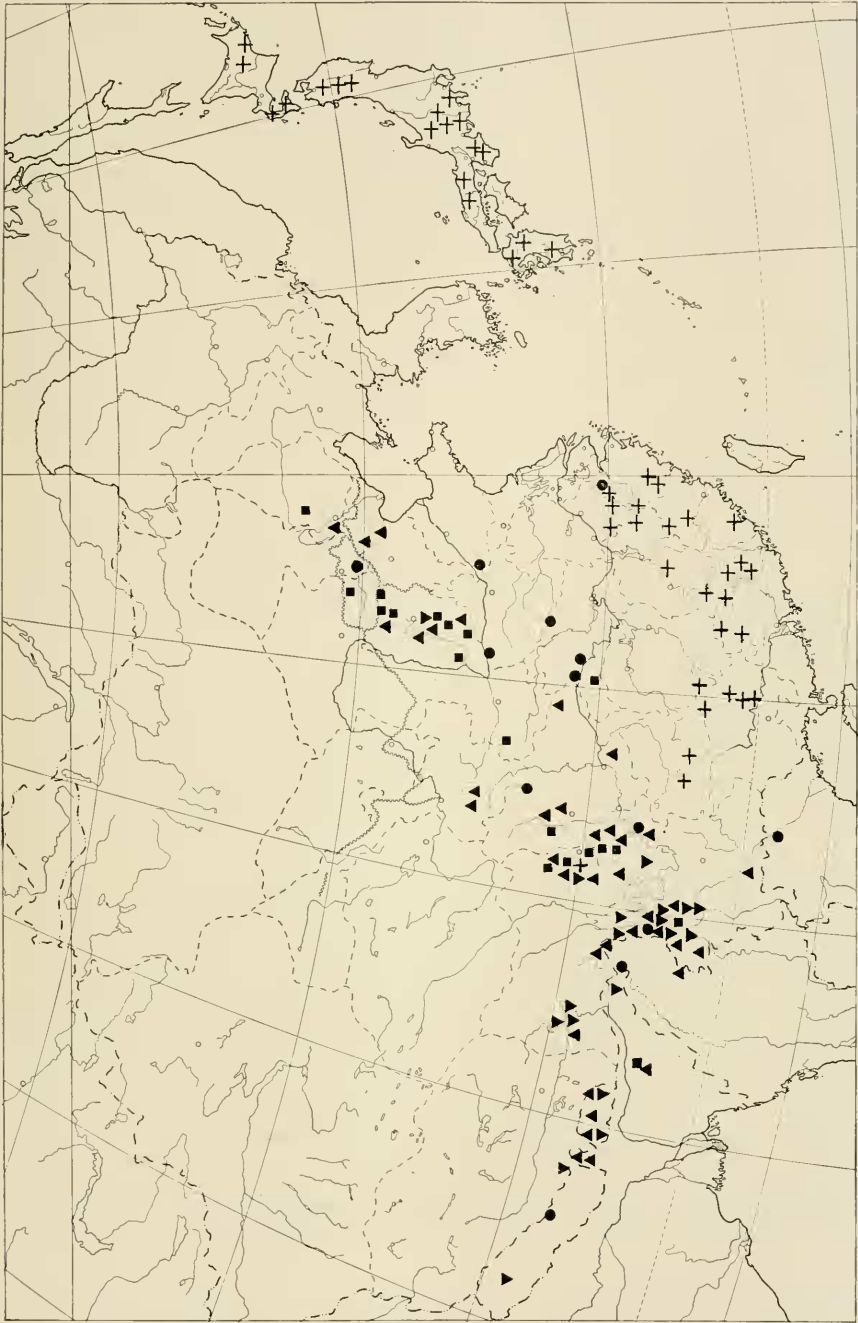
ILLUSTRATIONS:

H. H. Hu & W. Y. Chun. 1933. *Icones Plantarum Sinicarum*, fasc. III, pl. 136.

Siebold and Zuccarini. 1839 or 1840. *Flora Japonica*, table 61.

Gleason, H. A. 1952. *Illustrated Flora of the Northeastern United States and Adjacent Canada*, 2: 275.

DISTRIBUTION: In woods, mixed forests or open places, in southeastern China, from 500 to 1,000 meters, on the islands of Kyushu, Honshu, and Hokkaido in Japan, from sea level to 1,200 meters. (See Map 7.) CHINA. ANHWEI: Chuhuashan, Hwang Shan, Kimen. CHEKIANG: Changshan, Ping Yung, Taishun, Tienmu Shan, Tsingtien. FUKIEN: Shaowu, Nanping, Amoy. HUNAN: Yun-shan. KIANGSI: Fencheng, Kiennan, Kuling (in Lu Shan), Lungnan dist., Lu Shan, Ningdu, Wuyuen, Yutu. KWANGSI: Kweilin dist., Lingchwan dist., San-Chiang, Tzu-yuan, Yao Shan. KWANGTUNG: Linhsien, Lokchong, Meihsien, Yingtak, road to Chang Kiang, Kau Fung, Maan Chi Shan, Yao Shan, Lung T'au near Iu, Fungwan, Yam No Mt., Tsing Leung Shan, Tsing Wan Shan, between Bei Shen and Nan Shung. KWEICHOW: Kweiting, Kweiyang, Pachai, Tsingchen, Monts de Loutsongkoan, Ganpin, Mantsanping. SIKANG: Paohsing. YUNNAN: Pinfa-Tuchang. JAPAN. HONSHU ISLAND: Nagano Prefecture: Kose, Karuizawa, Shinano. Gumma Prefecture: Yokogawa. Nagano-Gumma border, Asama-yama. Aomori Prefecture: Mt. Iwaki, Ikarigaseki, Hakkoda-yama, Tanabu.



MAP 7. Distribution in eastern Asia of + *Hydrangea paniculata*, ■ *Hydrangea heteromalla*: ■ glabrous, ▲ pubescent, ▼ tomentose, ● pubescence not determined.

Shizuoka Prefecture: Subashiri, Shimoda, Fuji-yama. Nara Prefecture: Odaigahara-san, Omine-sammyaku. Tochigi Prefecture: Mt. Takodate, Lake Chuzenji, Nikko. Kyoto Prefecture: Yase. Gifu Prefecture: No locality. Wakayama Prefecture: Koyasan. Hyoga Prefecture: Ikuno. Kanagawa Prefecture: Hakone Mts., Yokohama. Yamaguchi Prefecture: Sengoku. Niigata Prefecture: Mt. Tanigawa, Shimizu. Akita Prefecture: Azuma. Yamagata Prefecture: Yamagata. HOKKAIDO ISLAND: Oshima Subprefecture: Hakodate, Todohokke, Fukayama. Ishikari Subprefecture: Sapporo, Tokobuchi, Otaru. Abashiri Subprefecture: Nokkeushi, Rubeshibe. Nemura Subprefecture: Nishiwada. Kushirokoku Subprefecture: Bokke. Shiribeshi Subprefecture: Otani. KYUSHU ISLAND: Kagoshima Prefecture: Mt. Kirishima, Kirishima National Park, Sakura-jima, Mt. Onamika, Yakushima. Nagasaki Prefecture: Nagasaki, Unzen. Fukuoka Prefecture: Okuma-san. Oita Prefecture: Beppo. SOVIET FEDERATED SOCIALIST REPUBLIC: SAKHALIN: Korsakov, Toronaiba.

DISCUSSION: *Hydrangea paniculata* is distinguished from the other Asiatic species of the section *Hydrangea* by its pyramidal inflorescence. This type of inflorescence is found elsewhere in *H. quercifolia* of the eastern United States. In flower and fruit *H. paniculata* is most like *H. heteromalla*; in fact, in regard to these characters, the two are almost indistinguishable, their only difference being the somewhat longer calyx lobes and the somewhat smaller seeds of *H. heteromalla*. Both have a half superior ovary with the styles united for one-half or more of their total length and alternately long and short stamens with filaments broadened toward their bases. *H. paniculata* is a fairly uniform species, showing no particular variation in any of its parts throughout its geographical range.

Hydrangea Schindleri was described by Engler (1930) in his key to the species of *Hydrangea*. He said of *H. Schindleri* that it is related to *H. chinensis* Maximowicz, has long lanceolate leaves constricted in the lower third and narrowly obovate sepals on the sterile flowers, and is found in the Kuling Mountains in Kiangsi, China. According to Rehder (Journal Arnold Arboretum, 14: 202-203, 1933), there were in the Herbarium at Berlin four specimens labeled *H. Schindleri*, all collected by A. K. Schindler in August and September, 1908, at Lu-Shan in the Kuling Mountains. Duplicates of these specimens were seen by the writer in various European herbaria. Two of the collections, *Schindler* 325 and 327, are *H. scandens* subsp. *chinensis*, and the other two, numbers 322a and 324, are *H. paniculata*. Engler did not designate a holotype, therefore, Rehder selected number 324 as the lectotype of *H. paniculata*.

10. *Hydrangea heteromalla* D. Don, Prodrum Florae Nepalensis, 211. 1825.

- Hydrangea vestita* Wallich, Tentamen Florae Nepalensis, 2: t. 49. 1826. Type from Nepal, Gosainthan, Wallich Catalogue No. 440/2 (K-W).
- Hydrangea khasiana* Hooker f. & Thomson, Journal Linnaean Society of London, Botany, 2:76. 1858. Type from Assam, Hooker & Thomson August 2, 1850 (holotype and isotypes K).
- Hydrangea vestita* Wallich var. *pubescens* Maximowicz, in Mémoires Académie impériale des Sciences de St. Pétersbourg, ser. 7, 10(16): 10. 1867. Two syntypes collected near Pekin by Tatarinow and Kirilow are cited. Not seen by the writer.
- Hydrangea Bretschneideri* Dippel, Handbuch der Laubholzkunde, 3:320. 1893. Named from cultivated material.
- Hydrangea peckinensis* Hort. ex Dippel, l. c., as synonym of *H. Bretschneideri*.
- Hydrangea mandarinorum* Diels, in Engler's Botanische Jahrbücher für Systematik, 29:372. 1900. Type from Nanchuan, Szechuan, Bock & von Rosthorn 1932 (photo and fragment of holotype A).
- Hydrangea Giralddii* Diels, l. c., p. 373. Five syntypes cited, all collected in Shensi province by Giralddi, Kishan, 1167, 1171; Tue lian pin, 1168; Taipai shan, 1169, 1172. Of these the writer has seen only a photo and fragment of No. 1167 (A).
- Hydrangea xanthoneura* Diels, l. c. Type from Nanchuan, Szechuan. Bock & von Rosthorn 354 (photo and fragment of holotype, isotype W).
- Hydrangea xanthoneura* var. *setchuenensis* Rehder in Mitteilungen Deutsche Dendrologische Gesellschaft, 21:186. 1912. Type from Wenchuan, Szechuan, Wilson 1323 (holotype A).
- Hydrangea Bretschneideri* Diels var. *setchuenensis* Rehder, Plantae Wilsonianae, 1:28. 1913. (Based on the preceding.)
- Hydrangea Bretschneideri* Diels var. *lanceifolia* Rehder, l. c. Type from Kangting (Tachien-lu), Sikang, Wilson 2412 (holotype A).
- Hydrangea Bretschneideri* Diels var. *Giralddii* Rehder, l. c., p. 39. (Based on *Hydrangea Giralddii* Diels.)
- Hydrangea xanthoneura* Diels var. *Wilsonii* Rehder, l. c., p. 27. Type from near Kangting (Tachien-lu), Sikang, Wilson 2407 (holotype A).
- Hydrangea heteromalla* D. Don var. *mollis* Rehder, l. c., p. 151. Type from Tsang chan near Tali, Yunnan, Delavay 1148 (holotype P, fragment and photo A).
- Hydrangea hypoglauca* Rehder, l. c., p. 26. Type from Ichang, Hupeh, Henry 6056 (holotype A, isotypes G, P, E, BM).
- Hydrangea pubinervis* Rehder, l. c., p. 27. Type from Wa Shan, Szechuan, Wilson 2411 (holotype A, isotypes E, K, BM, W).
- Hydrangea dumicola* W. W. Smith, Notes, Royal Botanic Garden, Edinburgh, 10:39. 1917. Three syntypes are cited from Yunnan: Mingkwong Valley, Forrest 8705 (E, K), 8391 (A, E, K), Tengyueh, Howell 51 (E).
- Hydrangea macrocarpa* Handel-Mazzetti, Anzeiger der mathematisch-naturwissenschaftlichen Classe: Kaiserliche Akademie der Wissenschaften. Wien, 62:144. 1925. Type from Hweili, Sikang, Handel-Mazzetti 5156 (holotype W, isotypes E, WU).
- Hydrangea heteromalla* D. Don var. *parviflora* Marquand & Shaw, Journal Linnaean Society of London, Botany, 48:183. 1929. Type from near Gyala, Tibet, Ward 5953 (holotype K).

Hydrangea sungpanensis Handel-Mazzetti, *Symbolae Sinicae*, 7:444. 1931. Type from Sungpan, Szechuan. *Weigold. June-August, 1914* (holotype W).

Much branched shrub or small tree, 0.5 to 7 m. tall; branchlets and inflorescence pubescent with upwardly appressed hairs 0.5–1 mm. long; leaves ovate, often broadly so, 8.5–21.5 cm. long, 3–14 cm. wide, 1.5 to 3 times as long as wide, lower surface pubescent with varying amounts of hairs from sparse to dense enough to cover surface of leaf, or sometimes nearly glabrous with hairs along veins only; upper surface with a few scattered hairs or glabrous; petiole 2.5–4 cm. long, pubescent as the stem; inflorescence a rounded, many-branched cluster, 8–30 cm. broad; bracts linear to lanceolate, chartaceous, 1–3 cm. long, 2–5 mm. wide, few pili on back and along margins; fertile flowers white, numerous; hypanthium 0.7–1.5 mm. long; calyx lobes 5, deltoid, 0.8–3 mm. long; petals 5, 2–3.2 mm. long, 1 mm. wide, ovate, falling separately; stamens 10, rarely 12, 2–6 mm. long, filaments broadened toward base; ovary half superior; styles 3 or 4, 1.5–2 mm. long, united for 0.5–0.8 mm.; capsules 4–5.5 mm. long, hypanthium 1.5–3 mm. long, styles 2–3.2 mm. long, united for 1–2.2 mm., about $\frac{1}{2}$ to $\frac{3}{4}$ of their length; seeds 1.5–2 mm. long, elliptical, tapering at each end into minute tail-like extensions; sterile flowers always present, white, sepals 4, 1–3 cm. in diameter. (See plate 5, figure 2.)

TYPE LOCALITY: Nepal, Gosainthan. Type collection: *Wallich in 1821*, No. 440/2 of Wallich's Catalogue. Holotype K-W, a specimen from the Hooker Herbarium at Kew, collected by Wallich in Nepal but without a Catalogue number. Specimens bearing Wallich Catalogue No. 440, from other herbaria (C, P, BM) may be isotypes.

ILLUSTRATIONS:

H. H. Hu & W. Y. Chun. *Icones Plantarum Sinicarum*, fasc. I, plate 27, 1929, as *H. Bretschneideri*; and fasc. III, plate 137, 1930, as *H. xanthoneura*.

N. Wallich. *Tentamen Florae Nepalensis*, t. 49, 1826, as *H. vestita*.
New Flora and Silva, 1: figure 81, 1929, as *H. Bretschneideri*.

DISTRIBUTION: Mixed forests, thickets and open places, west central to northeastern China and the Himalayas. (See Map 7.) CHINA. CHAHAR: Chohn, *p*.⁶ CHEKIANG: Tien-mu-shan. HONAN: Tsai-Yuan Hsien; Lushih Hsien. HOPEH: Peiping, *p*; Po-hua-shan, *p, g*; Tehe-Ly, Tang Ho, Pei Nin Ting Mt., *p*; Siao Wu Tai Shan, *p*; Keang Hsuai Ho, *p*; Fu-ling-hsien; Tientsin; Ling Shan, *p*. HUPEH: Fanghsien; Hingshan; Ichang, *g*; Patung; Kienshih, *g*; Huan Tsao. INNER MONGOLIA: Wulashan, *g*. JEHOL: Weichang, *p*; near Hsing Lung Shan, *p*. KANSU: Choni district (Tao River

⁶ The small letters, *p, g, t*, following the place names refer to the vesture of the lower leaf surface; *p*-pubescent, *t*-tomentose, *g*-glabrous.

basin), *p*; Liehen, *p*: Old Taochow; Tatung River; Lower Tebbu Country, *p*, *g*; Kwan-schan near Lung, *g*; Sin long chan and Ma ho chan, *p*. KWANGTUNG: Fuchai. PINGYUAN: Tsiyuan. SHANSI: Chinyuan, *p*, *g*; Kiehshu, *g*; Luya Shan, *g*; Ning-wu, *g*; Wuchai, *p*, *g*; Tanpa district, *p*; Yaan, *p*; Hweili, *t*; Yenyuan, *t*. SUIYUAN: No locality. SZECHUAN: Chengkow, *p*; Dzampersheren, *p*; mountains of Kulu; "Muli Kingdom," *p*; Kwanhsien, *g*; Lifan, *p*; Maohsien, *p*; Mt. Mitzuga, *p*; Nanchwan, *p*; Mt. Omei, *p*, *g*; Opien, *g*; Mo-tien-ling, *g*; Tenghsiang-ying, *g*; Tsien-chuan-fiu, *p*; Sungpan, *p*. YUNNAN: Champutong; Chenkang, *p*; Chungtien, *p*, *t*; Mt. Dyalnko, *t*; Mt. Kaakerpu, *t*; Lanping, *g*; Likiang, *p*, *t*; Mengtsz, *p*; Teng-yueh, *p*; Weisi, *p*, *t*; Pe-long-tsin, *t*; Tong-Tchouan, *t*; Ma-hong, *g*; Pe yen tsin, *t*; Chi-tse-lo, *p*; Yong-shan, *g*; Kiukiang Valley, *t*; Buehlwang Valley; Wenshan; east flank Tali Range, *t*; Tali, *t*; Tsang chan near Tali, *t*; Mingkwong Valley, *p*; Mekong-Salween divide, *t*; Shweli-Salween divide, *t*, *p*; Salween River at 27°58'. INDO-CHINA. TONKIN: Chapa. BHUTAN. Singhi Djong, *p*; Shabjetong, *t*; Bumthang, *p*; Trashieho Djong, *p*; Bela La near Paro, *p*; Gyetsa to Juto La, *t*; Paro; Sinehu La, *g*; Zado La, *g*; Fujudin, *g*; Chapcha, *t*; Mirchoma; Gyasa Djong, *p*. BURMA. Hpimaw, *p*; Adung Valley, *p*; Mungku Hkyet; Shing Hong Torrent, *p*; Chawehi. NEPAL. Mailoong Pati, *p*; Gosainthan; Jumla, *p*; Chankheli Lagna, *p*; Tarakot, Bheri River, *t*; Sialgarhi, *p*; Langtang. TIBET. Cha Gyamda Chu, *t*; Nayu Chu, *p*; Kongbo Province, Je Pasum Lake, *t*; Lushu Chu, *t*; Tsangpo Valley, *t*; gorge of Tsangpo near Gyala, *t*; Ka Gwr pu Temple, *t*; Laktang, *g*; Ngawchang Valley, *g*; above Litang R., *p*, Yatung, *t*, Lenda Khala, *t*; valley of the Seingku, *p*. INDIA. ASSAM: Delei Valley, *t*; Khasia Hills, *g*; Surureem, *p*; Moflong; Boga Panee, *p*; Kala Panee. SIKKIM: Kaljorinie, *p*; Lachen Valley, *p*. WEST BENGAL: Darjeeling, *p*; Tankra Mt.; Kalapohri, *p*; Tumbok. UTTAR PRADESH: Kumaun District, Kuthie, *p*; Garhwal, *t*.

DISCUSSION: *Hydrangea heteromalla*, unlike the closely related *H. paniculata*, varies throughout its range in leaf shape and vesture. The names listed in synonymy were all based on such variants and none is worthy of recognition. *Hydrangea xanthoneura* and *H. Bretschneideri* are probably the best known of these names, but those workers recognizing both of these as constituting separate species had difficulty separating them. Rehder (1924) said of the two that they "are very closely related and both vary with pubescent and glabrescent leaves; the only reliable character to distinguish these two species is apparently the behavior of the bark which in *H. Bretschneideri* separates in the second year in thin flakes and is of chestnut brown color, without or with few inconspicuous lenticels, while in *H. xanthoneura* the dark adheres to the branch, is conspicuously lenticellate and varies from yellow gray to red brown in color." However, he separated *H. xanthoneura* by the glabrous or glabrescent underside of

the leaves which are more or less cuneate at the base. Of *H. Bretschneideri* var. *lancifolia* he said (1911, p. 28), "This variety might possibly be considered a pubescent and narrow leaved form of *H. xanthoneura*, since it has almost the same kind of bark as var. *Wilsonii* of that species."

Don based his *Hydrangea heteromalla* on a specimen collected by Wallich at Gosainthan in Nepal. This Wallich specimen, as in the case of the one cited for *H. anomala* Don, is not in the Lambert Herbarium at the British Museum but is in the Wallich Herbarium at Kew. There are three specimens in the Wallich Herbarium written up as follows in Wallich's Catalogue:

"440 *Hydrangea vestita* Wall. in Herb. 1824.

1. Kumaon, R. B.

2. Napalia 1821

β fimbriata, Napalia, 1821."

Of these three specimens, one of them, 440/2 was collected at Gosainthan by Wallich. This specimen consists of a branch with a full inflorescence and a small piece of infructescence. The latter does not belong with the inflorescence, but is *H. aspera*. The flowering branch, with leaves tomentose beneath and more or less rounded, and with entire sterile flowers, agrees with Don's description of *H. heteromalla*, which he stated was collected at Gosainthan. Most probably this specimen is the type of *H. heteromalla*. Of the other two specimens included under No. 440, one, 440/1, was collected in "Kumaon" by Robert Blinkworth. On this sheet are an inflorescence and an infructescence of *H. aspera* and a small piece of infructescence, which does not belong to the other material, but is *H. heteromalla*. The third specimen, 440 β fimbriata was collected by Wallich in 1821. It is *H. aspera*. The mixture of these two species in the Wallich material is no doubt in part responsible for the confusion regarding the later mistaken interpretations of *H. vestita* Wallich, *H. heteromalla* Don, and *H. aspera* Don.

Hydrangea vestita Wallich was published in the *Tentamen* on plate 49, without a description. The plate, which is the type for the name, shows a flowering branch (the dominant element of the plate) and a small piece of a fruiting branch. The details of the flower and fruit structure on this plate are not clear, but by comparing this plate with a painting in the East India Company's collection of paintings in Herb. Kew, it becomes evident that two elements are represented in the original painting, and that the plate was adapted from it. The dominant element, both in the painting and the plate in the *Tentamen*, a branch with a full inflorescence, is surely what Wallich intended his *H. vestita* to be. The lesser element, the piece of infructescence, is *H. aspera*. Comparison of this plate with the Wallich specimen No. 440/2, described above as consisting of a full inflorescence of *H. heteromalla* and a small infructescence of *H. aspera*,

shows that the plate with its mixture of the same two species was made from the specimen. It may be concluded that this specimen served as the basis of *H. heteromalla* Don and later for the plate of *H. vestita* Wallich.

The material on which *Hydrangea khasiana* is based was collected by Hooker and Thomson in the Khasia Mountains at Surureem in the valley of the Kala-panee River. Hooker and Thomson said of it that it differs from "*H. vestita*," that is *H. heteromalla*, by its more robust habit and its broader leaves, which are cordate at the base. *H. heteromalla* varies in habit from a shrub to a small tree. Its leaves are also variable. The variation shown by *H. khasiana* is not significant.

Maximowicz (1867) based *Hydrangea vestita* var. *pubescens* on two specimens collected by Tatarinow and Kirilow in the Peking area of northern China. The collections of both of these men were eventually deposited in the herbarium of the Botanic Garden in St. Petersburg, where they were available to Maximowicz for study. Maximowicz stated that his proposed variety was conspecific with the Himalayan *H. vestita* (referred in this paper to *H. heteromalla*) and he followed Hooker and Thomson in using the name *H. vestita* instead of *H. heteromallaa* for the Himalayan plant. Since he stated⁷ that he saw the Wallich specimen from Gosainthan on which *H. vestita* Wallich was based, there is no doubt that he used the name *H. vestita* var. *pubescens* for the species here referred to *H. heteromalla*. However, he took the varietal epithet from *H. pubescens* Decaisne (Flore des Serres, 4: t. 378, 1848). He stated that this name, known to him only from the illustration, was not different from his proposed variety. Decaisne's *H. pubescens*, however, was described from a cultivated plant grown from seed which was said to have come from Japan. The illustration representing this plant does not show any detail of flower structure and no specimen is cited in the description. Therefore, it is not possible to identify the plate, other than to say that if the plant shown were grown from seed of Japanese origin it would not be the same as Maximowicz's *H. vestita* var. *pubescens*, which is based on the two collections from Peking. It seems best, therefore, to regard the name *H. pubescens* Decaisne as a *nomen dubium*.

Hydrangea Bretschneideri was named by Dr. Leopold Dippel, who was director of the botanical garden in Darmstadt, Germany. Dippel stated, in his description of this plant, that it was grown from seed sent from Peking by Dr. Bretschneider, that it had been referred to by the names *H. vestita* and *H. pekinensis*, and that it was sometimes confused with *H. pubescens* Decaisne. Dippel did not cite a specimen in his description of *H. Bretschneideri*; hence no type specimen was designated.

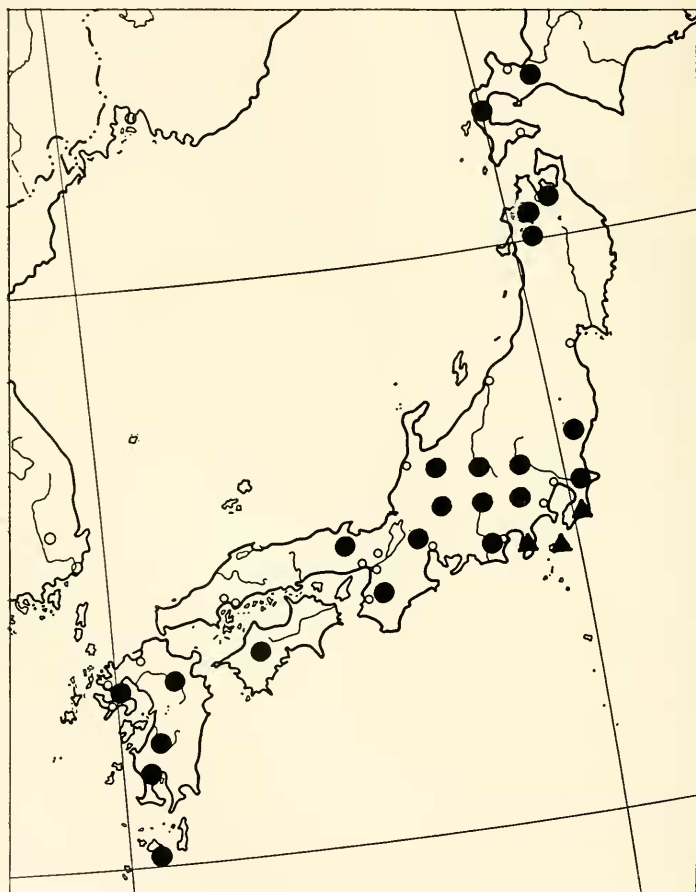
⁷ See Maximowicz (1867, p. 10): "Ipsi vidi e Kumaon, Gossainthan (ex hb. Lambert) et spec. Wallich No. 440, flor. et frf."

However, cultivated specimens grown in the garden at Darmstadt have been distributed to various herbaria (*Koehne 470* and *Purpus June 15, 1924* are both in the herbarium of the Arnold Arboretum.) These specimens labeled "*Hydrangea bretschneideri* Dippel" doubtless represent the species described by Dippel.

Subsection 6. MACROPHYLLAE

Hydrangea, sect. *Hydrangea*, subsect. *Macrophyllae* McClintock, Journal Arnold Arboretum, 37:374. 1956.

Hydrangea, sect. *Euhdrangea*, series 2. *Piptopetalae* Maximowicz, Mémoires Académie impériale des Sciences de St. Pétersbourg, ser. 7, 10(16): 8 (Revisio Hydrangearum Asiae Orientalis). 1867. In part.



MAP 8. Distribution in Japan of

● *Hydrangea macrophylla* subsp. *serrata*

▲ *Hydrangea macrophylla* subsp. *macrophylla*

Hydrangea, subgenus *Euhydrangea*, sect. *Japonico-Sincensis*, subsect. *Piptopetalae* (Maximowicz) Schneider, Handbuch der Laubholzkunde, 388. 1905. In part.

Flowers white, blue, or pink; ovary inferior in anthesis, half superior in fruit; capsule conical at apex; styles about same length as conical disk; seeds caudate. A single species, *Hydrangea macrophylla* (Thunberg) Seringe, widespread in eastern Asia.

11. ***Hydrangea macrophylla*** (Thunberg) Seringe in DeCandolle, Prodrumus, 4: 15. 1830.

Viburnum macrophyllum Thunberg, Flora Japonica, 125. 1784.

Shrubs 1–3 m. tall; branchlets and inflorescence glabrous or pubescent with upwardly curled hairs; leaves 5.5–19 cm. long, 2.5–13 cm. wide, their length about 1.5 to 4 times their width, ovate or broadly ovate to more or less obovate, texture varying from thin to thick; petioles 1–4 cm. long; bracts none; inflorescence a flat-topped, compound, several-branched cluster; fertile flowers white; hypanthium 1.2–2 mm. long; calyx lobes 5, deltoid, 0.5–1 mm. long; petals 5, 2–3 mm. long, reflexed before falling; stamens 10, 2–6 mm. long; styles usually 3, occasionally 2, 4 or 5, 1–2 mm. long, in early anthesis free to base, ovary then inferior; styles in late anthesis united for 0.3–1 mm. from base, ovary then half superior; base of ovary and capsule, sometimes tapered toward pedicel; capsule (including styles) 2.5–8 mm. long, hypanthium 1.5–5 mm. long, styles 1.2–3.5 mm. long, free portion of styles 0.7–1.5 mm., united portion of styles 0.5–2 mm. long; seeds 0.5–0.7 mm. long; sterile flowers white or blue; petaloid sepals 1–3 cm. across, entire or serrate. (See plate 6, figures 2 and 3.)

DISTRIBUTION: The eastern Himalayas, southern China, and Japan. (Map 8 shows distribution in Japan.)

KEY TO THE SUBSPECIES OF *HYDRANGEA MACROPHYLLA*

1. Stems and leaves hispid with spreading hairs 1–3 mm. long. d. subsp. *Chungii*
1. Stems and leaves glabrous or pubescent with hairs less than 1 mm. long.
 2. Petals 3–4 mm. long; styles in anthesis 2 mm. long; capsules 6–8 mm. long; leaf length about one and one-half times greater than width.
 - a. subsp. *macrophylla*
 2. Petals 2–3 mm. long; styles in anthesis 1–2 mm. long; capsules 2.5–6 mm. long; leaf length one and one-half to four times greater than width.
 3. Capsules 2.5–5 mm. long, with styles 1.2–2.5 mm. long, free portions 0.7–1.5 mm. long. (Plants of Japan.)
 - b. subsp. *serrata*
 3. Capsules 4–6 mm. long, with styles 2–4 mm. long, free portions 1.5–2 mm. long. (Plants of the eastern Himalayas and southern China.)
 - c. subsp. *stylosa*

11a. ***Hydrangea macrophylla*** subsp. ***macrophylla***.

Hydrangea macrophylla (Thunberg) Seringe in DeCandolle, Prodrumus, 4: 15. 1830.

Viburnum macrophyllum Thunberg, *Flora Japonica*, 125. 1784.

Hydrangea macrophylla var. *normalis* Wilson, *Journal Arnold Arboretum*, 4:234. 1923. Type from Japan, *Suzuki July 1917* (holotype A).

Hydrangea maritima Haworth-Booth in *The Hydrangeas*, p. 38. 1950. (Based on *Hydrangea macrophylla* var. *normalis*.)

Branchlets, inflorescence, and leaves glabrous; leaves 7.5–19 cm. long, 4–13 cm. wide, their length about 1.5 times their width, broadly ovate to more or less obovate, margins coarsely serrate, texture “thick”; petioles 4 cm. long; petals 3.5–4 mm. long; stamens 3.5–4.5 mm. long; styles 3, 2 mm. long in early anthesis; capsules (including styles) 6.5–8 mm. long, hypanthium 3.5–5 mm. long, styles 2.5–3.5 mm. long, united portion of styles 1.5–2 mm. long, free portion of styles 1–1.5 mm. long.

DISTRIBUTION: Japan. Chiba (Boso or Boshu) Peninsula on the coast of east central Honshu and the islands of Oshima (De Vries) and Hachijo, from sea level to 150 meters.

TYPE LOCALITY of *Viburnum macrophyllum*: Japan. Type collection: four syntypes collected by Thunberg. According to Hara (1955) two were collected in Japan and two were collected in Thunberg's garden in Uppsala. All specimens belong to a garden form having nearly all sterile flowers in its inflorescences.

SPECIMENS EXAMINED: JAPAN. HONSHU ISLAND. Tokyo Prefecture: Hachijo Island, Oshima, Chiba (Boso or Boshu) Peninsula.

11b. *Hydrangea macrophylla* (Thunberg) Seringe subsp. *serrata* (Thunberg) Makino in *Journal of Japanese Botany*, 6(7):11. 1929.

Viburnum serratum Thunberg, *Flora Japonica*, 124. 1784.

Hydrangea serrata (Thunberg) Seringe in DeCandolle, *Prodromus*, 4:15. 1830.

Viburnum cuspidatum Thunberg, *l. c.* 125. Type from Japan, collected by Thunberg (UPS).

Hydrangea cuspidata (Thunberg) Miquel, *Annales Museum Botanicum Lugduno-Batavum*, 3:98. 1867.

Hydrangea yesoensis Koidzumi, *Botanical Magazine, Tokyo*, 40:347. 1926. Type from Hakodate, Hokkaido, *Maximowicz in 1861* (isotypes US, K, S, W, NY).

Branchlets, leaves, and inflorescence glabrous or pubescent with upwardly appressed hairs; leaves 5.5–15 cm. long, 3–6 cm. wide, their length 1.5 to 3 times their width, ovate, acute or acuminate at apex; petioles 1–3 cm. long; hypanthium 1.2–1.3 mm. long; calyx lobes 5, 0.5–0.6 mm. long; petals 2–3 mm. long; stamens 2–5 mm. long; styles usually 3, occasionally 2 or 4, 1–1.7 mm. long in early anthesis; styles united for 0.3–1 mm. from base in late anthesis; capsule (including styles) 2.5–5 (rarely 6) mm. long, united for 0.5–1.5 mm., free portion of styles 0.7–1.5 mm. long.

TYPE LOCALITY of *Viburnum serratum*: Japan. Type collection: five syntypes in the Thunberg Herbarium, specimen δ selected as lectotype by Hara (1955).

DISTRIBUTION: Japan and southern Korea, in woods and forests usually in mountainous areas, at elevations of 70 to 1,500 meters. JAPAN. HONSHU ISLAND. Hyogo Prefecture: Arima. Aichi Prefecture: Shinano. Gifu Prefecture: no locality. Gumma Prefecture: Ikaho, Mt. Haruna. Tochigi Prefecture: Nikko to Lake Chuzenji, Lake Chuzenji, Nikko. Ibaraki Prefecture: Mt. Kaba. Kanagawa Prefecture: Hakone Mts., Manazuru, Nagoa, Miyanoshita, Yokohama, Sagami Bay. Kyoto Prefecture: Ohara, Kuramayama. Wakayama Prefecture: Koya. Yamagata Prefecture: Ubayu. Yamanashi Prefecture: Lake Shoji, Jizoga-take, Nambu. Nara Prefecture: Mt. Omine. Nagano Prefecture: Karuizawa, Kisokoma-ga-take, Norikura, Agawa, Kawagishi, Otake River, Asama-yama. Shizuoka Prefecture: Shojiko, Shimoda. Saitama Prefecture: Mt. Bukō, Mitake, Izuga-take, Hikawa, Shimura, Mt. Mitsumine. Niigata Prefecture: Mt. Tanigawa, Sado Island. Osaka Prefecture: Mt. Kongosan. Akita Prefecture: no locality. Tokyo Prefecture: Tokyo. Aomori Prefecture: Hakkadayama, Lake Towada, Hirosaki. KYUSHU ISLAND: Nagasaki Prefecture: Tsu-shima. Kagoshima Prefecture: Mt. Kirishima. Oita Prefecture: Kujisan. Fukuoka Prefecture: Mt. Ukidake. SHIKOKU ISLAND: Kochi Prefecture: Shimonanokawa, Takaoka, Shiraga-yama, Engyoji. HOKKAIDO ISLAND: Oshima Subprefecture: Hakodate, Ichinowatari. Ishikari Subprefecture: Garugawa, Moiwadake, Teine-yama. Shiribeshi Subprefecture: Shiribeshi san. KOREA. QUELPAERT ISLAND.

- 11c. ***Hydrangea macrophylla*** (Thunberg) Seringe subsp. ***stylosa*** (Hooker f. & Thomson) McClintock, *Journal Arnold Arboretum*, 37: 373. 1956.

Hydrangea stylosa Hooker f. & Thomson, *Journal Linnaean Society of London, Botany*, 2: 75. November 1857 (holotype K).

Hydrangea cyanema Nuttall in Curtis's *Botanical Magazine*, t. 5038. March 1858. Described from cultivated material.

Hydrangea taroensis Handel-Mazzetti, *Anzeiger der mathematisch-naturwissenschaftlichen Classe: Kaiserliche Akademie der Wissenschaften. Wien*, 62: 144. 1925. Type from near Tibet-Burma border, Irrawadi River, *Handel-Mazzetti 9455* (holotype W, isotypes A, E).

Hydrangea kwangsiensis Hu, *Journal Arnold Arboretum*, 12: 152. 1931. Type from Kwangsi, *Ching 5836* (photos and fragments of holotype A, NY, isotype W).

Hydrangea indochinensis Merrill, *Journal Arnold Arboretum*, 23: 167. 1942. Type from Chapa, Indochina, *Petelot 2687* (holotype A).

Branchlets, leaves and inflorescences glabrous or pubescent with upwardly curled hairs; leaves ovate, 7.5–14.5 cm. long, 2.5–5.5 cm. wide, length

two to four times as great as width; leaf margins finely to coarsely serrate or entire; petioles 0.7–3 cm. long; fertile flowers lavender or blue; petals 2 mm. long; stamens 4–6 mm. long; styles 3, 4, or 5, 1.5 mm. long; capsules (including styles) 5–6 mm. long, hypanthium 2–3 mm. long, styles 2–3 mm. long, united for 0.5–1.5 mm., free portion of styles 1.5–2 mm.

TYPE LOCALITY of *Hydrangea stylosa* Hooker f. & Thomson: India, Sikkim, Lachen (8,000 ft.). Type collection: *Hooker, August 4, 1849* (holotype K).

ILLUSTRATIONS:

H. H. Hu and W. Y. Chun. 1933. *Icones Plantarum Sinicarum*, fasc. III, pl. 135, as *H. kwangsiensis* Hu.

Curtis's Botanical Magazine, 1858. Table 5038, as *H. cyanema* Nuttall.

DISTRIBUTION: Forests and wooded areas in the eastern Himalayas of Bhutan and Sikkim and mountains of Yunnan, Kwangsi, Kweichow, Kwangtung and Indochina, at elevations of 500 to 3,300 meters. CHINA. KWANGSI: Chu-feng Shan, north of Luchen Hsien on border of Kweichow, Ling Wang Shan. KWANGTUNG: Yao Shan. KWEICHOW: Yao-ren-shan, San hoa. YUNNAN: Eastern flank of Tali Range; Yangpi Valley; western flank of Tali Range, Shweli-Salween divide; Tali Range at middle part of Chung Ho Mt.; Shweli River drainage basin to summit of Shweli-Salween watershed east of Tengueh; Shunning Hsien; Tali Hsien. BURMA. Irrawadi River, near Tibet-Burma border. BHUTAN. Tsanka to Chendehi; Trashiyangsi Chu; near Tongsa; Ridang near Tongsa; Rudong La; Kancham. INDIA. Sikkim: Talung, Lachen. INDOCHINA. Vietnam: Chapa.

DISCUSSION: *Hydrangea cyanema* Nuttall ex Hooker was described and illustrated in Curtis's Botanical Magazine, plate 5038, in 1858. Hooker stated that this plant was "introduced by Mr. Nuttall from Bhotan where it was discovered by Mr. Booth." Thomas J. Booth collected rhododendrons and other plants in the eastern Himalayas for his uncle, Thomas Nuttall of Nutgrove, Rainhill, Prescott. From Booth's seeds, a number of rhododendrons were grown and introduced into cultivation for the first time. The area of "Bhotan" where Booth collected is to the east of the present Bhutan, and appears to be in the Daphla (Dafla) and Aka Hills (see Stapf in Curtis's Botanical Magazine, t. 8078). In Herb. Kew is a fruiting specimen collected by Booth in "Bootan" and which, according to the label, was from "Herb. Nuttall." It probably was this collection that furnished the seed from which was grown the plant used for the illustration of *Hydrangea cyanema*. In the description which accompanies the illustration, no specimen is cited; therefore, the illustration may be considered to represent the type.

The specimen on which *Hydrangea kwangsiensis* was based, *Ching 5836*

from Kiangsi, and a second specimen, *Tsiang* 6285 from Kweichow, differ slightly in leaf margin and leaf texture from the other material included in subsp. *stylosa*. In most of the material of this subspecies the leaves are serrate and "thin" in texture, but the two specimens from Kiangsi and Kweichow have leaves which have entire margins and are somewhat "thick" in texture. These leaf differences are of a similar nature, but not as pronounced, as the leaf differences between the Japanese subsp. *serrata* and subsp. *macrophylla*.

Probably because of the small size of the fertile flowers, *Hydrangea macrophylla* subsp. *stylosa* has been confused with other species in the Himalayan region and in western China. For the same reason, perhaps, its relationship to *H. macrophylla* has been overlooked. It is of interest that this relationship extends the geographical range of *H. macrophylla* from the Himalayas through China and to Japan.

11d. ***Hydrangea macrophylla*** (Thunberg) Seringe subsp. ***Chungii*** (Rehder) McClintock, *Journal Arnold Arboretum*, 37: 374. 1956.

Hydrangea Chungii Rehder, *Journal Arnold Arboretum*, 12: 69. 1931.

Shrubs 1 to 2 m. tall; stems, branchlets and leaves hirsute with spreading hairs, 1.5–3 mm. long, in addition shorter, upwardly curled hairs along stem, 0.5 mm. long; leaves 10–19 cm. long, 5–8 cm. wide, 2 to 2.5 times as long as wide, petioles 1–4 cm. long; mature fertile flowers not seen; styles (in buds) 3 or 4, free to their bases; capsules 3 mm. long; hypanthium 1.8 mm. long; styles 1.2 mm. long, free portions 0.8 mm. long, united portions 0.4 mm. long.

TYPE LOCALITY: Yenping, Fukien. Type collection: *Chung* 3043 (holotype A, isotypes A, UC, K, W).

ILLUSTRATIONS:

H. H. Hu and W. Y. Chun. 1933. *Icones Plantarum Sinicarum*, fasc. III, plate 134, as *Hydrangea Chungii*.

DISTRIBUTION: Central Fukien, China. CHINA. Fukien: Yenping.

DISCUSSION: *Hydrangea macrophylla* subsp. *Chungii* is characterized by its hirsute stems and leaves. Of the two collections from Yenping one is in fruit and the other in flower. The flowers of this latter specimen are immature but because the styles are free to the base the plant is considered to belong to *H. macrophylla*. Known only from the three collections cited above the subspecies is doubtless restricted in its range.

DISCUSSION OF *Hydrangea macrophylla* AND THE ORIGIN
OF ITS GARDEN FORMS

Hydrangea macrophylla is probably the best known species of the genus because to it belong the many cultivated forms of the garden hydrangea. These forms with their sterile-flowered inflorescences represent an unusual condition of subsp. *macrophylla* found on the east central coast of the island of Honshu. *Hydrangea macrophylla* and *H. serrata*, long considered to be closely related Japanese species, were combined by Makino (1929) into a single species. Hara (1955) reviewed the nomenclatural problems involved in this combination. The two species from the Asiatic mainland, *H. stylosa* and *H. Chungii*, are combined here for the first time as subspecies of *H. macrophylla*. The relationship between subsp. *stylosa* and subsp. *serrata* is close and it is difficult to distinguish between the two. Subsp. *macrophylla* may be separated from the others by its larger flower parts and thick-textured leaves, and subsp. *Chungii* is separable by its hispid spreading hairs.

Within recent years the question of the origin of the garden forms of *Hydrangea macrophylla* has been discussed from two different points of view. Wilson (1923) suggested that the commonly cultivated form with the globose inflorescences consisting of all sterile flowers "is simply an anomalous condition of a littoral plant very common on the shores of Boshu peninsula in central Hondo, or Oshima or De Vries' Island, on Hachijo and others of the seven isles of Idzu, described in detail . . . under the name of *Hydrangea macrophylla* var. *normalis*." Wilson goes on to say that the "replacing of the ordinary flowers by sterile flowers having petaloid sepals occurs in several species of *Hydrangea* . . . it is probable that this character can and does appear as a sport in many species of *Hydrangea*." In 1917, Wilson found on Oshima a plant which he considered to be a wild prototype of the garden plant and which was no different from the plant which he knew so well, both at home and in China and Japan. Although the plant which Wilson found on the coastal area of central Honshu was growing not far from Yokohama and Tokyo, its relation to the cultivated hydrangeas had not been suggested until Wilson made his observations.

Wilson recognized his coastal plant as being different from *Hydrangea serrata*, the Japanese species most closely related to *H. macrophylla*, which he knew as a woodland plant growing in the mountains throughout Japan. Differences in the leaves between these two species, not readily seen in herbarium material, were pointed out by Wilson. He distinguished between the two in the field on the basis of their leaf textures and the greater vigor of *H. macrophylla*. The taxonomy of *H. macrophylla* and *H. serrata* has been complicated by the similarity between the two and by the cultivation of numerous garden forms of both. This similarity is so

strong that Japanese botanists, particularly Makino and Hara, consider them to be coastal and inland forms of the same species.

Haworth-Booth (1950) discussed the origin of the garden hydrangeas from the point of view of their being hybrids. He starts with the premise that there are three species from the woodland areas of Japan for which he used the following names: *H. acuminata*, *H. japonica*, and *H. Thunbergii*. He characterized these taxa chiefly on the basis of their habit and cultural responses, but also mentioned the shapes of the capsules and the color and margins of the enlarged sepals of the sterile flowers. According to him *H. acuminata* has capsules tapered to their bases and entire sepals which are "pink in neutral or limy soil and blue in acid soil"; *H. japonica* has capsules almost round and serrated sepals which "open white and then, absolutely irrespective of whether the plant is growing in neutral to limy or acid soil, turn crimson owing to the effect of sunlight"; *H. Thunbergii*, which is "earlier flowering and much more dwarf in growth with exceptionally numerous, tiny, orbicular ray-flowers of unusually vivid pink and reddish shoots (Haworth-Booth, 1950, p. 20). It is Haworth-Booth's contention that these three so-called species which share "certain characters such as woodland habit, the quality of flowering from all of the side shoots, and leaves that are thinner" in texture than the maritime form of *H. macrophylla* called var. *normalis* by Wilson, have hybridized to produce the plant which Thunberg described as *Viburnum serratum* and is here called *H. macrophylla* subsp. *serrata*. He further contended that these three woodland species, in addition to producing hybrids among themselves, have produced hybrids with the maritime plant described by Wilson under the name *H. macrophylla* var. *normalis*, and that from these hybrids have originated the plant which Thunberg described as *Viburnum macrophyllum* and which is here called *H. macrophylla* subsp. *macrophylla*. Haworth-Booth gave the name *H. maritima* to Wilson's *H. macrophylla* var. *normalis* because he considered Thunberg's name (*Viburnum macrophyllum*) to have been applied to a "hybrid race," and therefore, this epithet "cannot be used for a wild species which is only one of the ancestors of that hybrid race" (Haworth-Booth, p. 38).

From an examination of the available herbarium material and observations on living cultivated plants, it appears that the garden forms of *Hydrangea macrophylla* subsp. *macrophylla* are what Wilson said they were: an anomalous condition of the plant which he found in the coast of central Honshu. There is no evidence, morphological or otherwise, to substantiate Haworth-Booth's suggestion of there being three inland montane species of *Hydrangea* in Japan. He based his three "species" on plants named by Siebold and Zuccarini. The characters which Haworth-Booth ascribed to them were for the most part ecological and cultural

responses, such as tolerance to shade, flower color, time of flowering, habit of flowering, and texture of leaves. It is apparent that these are not morphological characters upon which species can be based. Doubtless, through mutation a plant or plants having all sterile flowers in their inflorescences appeared in the wild populations of both the montane and the maritime taxa, subsp. *serrata* and subsp. *macrophylla* respectively, such plants were selected for cultivation and from them have come the various garden forms.

The following names have been given to specimens of *Hydrangea* presumably of garden origin. From the descriptions and/or illustrations the names apply for the most part to *H. macrophylla* subsp. *macrophylla*.

Hortensia opuloides Lamarek, Encyclopédie Méthodique, Botanique, 3: 136, 1789. Based on a plant cultivated on Mauritius (Ile de France) and probably sent to the Jardin des Plantes in France by Commerson.

Primula mutabilis Loureiro, Flora Cochinchinensis 104, 1790. Merrill in his "Commentary on Loureiro's Flora Cochinchinensis" (Transactions American Philosophical Society, 24(2): 177, 1935) says "the description applies unmistakably to the commonly cultivated garden Hydrangea."

Hortensia japonica Gmelin in Linnaeus, Systema Natura, ed. 13, II, pt. 1, 722, 1791. Name only. Generic description based on that of Jussieu.

Hydrangea hortensis Smith, Icones Pietae Plantarum Rariorum, p. 12, t. 12, 1792. Through the agency of Sir Joseph Banks a living hydrangea was brought to Kew in 1789 from China. This plant was named *Hydrangea hortensis* by Sir James Smith who recognized it as being related to *H. arborescens* Linnaeus.

Hortensia mutabilis Schneevooft & Schwegman, Icones Plantarum Rariorum, t. 36, 1793. The illustration shows an inflorescence consisting entirely of sterile flowers which are violet or light purple in color. The dissections are not quite accurate but the plate surely represents a garden form of *Hydrangea macrophylla*.

Hydrangea Hortensia Siebold, Nova Acta: Academia (caesarea) Leopoldino-Carolina, 14(2): 688, 1829. Under this name Siebold cited as synonyms *Hydrangea hortensis* Smith, *Hortensia opuloides* Lamarek, and *Hortensia speciosa* Persoon. The plant, he stated, was cultivated in Japan, but he did not illustrate it in the Flora Japonica, perhaps because it was so well known.

Hydrangea japonica Siebold, l. c. 689. Siebold & Zuccarini, Flora Japonica 1: 106, t. 53, 1839 or 1840. Plant illustrated has pink fertile and sterile flowers. Siebold said of *Hydrangea japonica* that it was a garden plant cultivated for centuries in Japan but found in the wild state in the mountains of that country. He described it as having pink flowers, and

as being robust and large in all parts. The illustration shows it as being glabrous, this together with its robust habit suggests *H. macrophylla* subsp. *macrophylla* rather than *H. macrophylla* subsp. *serrata*, despite the fact that Siebold said that the plant grows wild in the mountains of Japan. Wilson cited this name as a synonym of his *H. macrophylla* var. *normalis* f. *rosea*, which he said "has pink, more or less toothed ray-flowers, otherwise it is very similar to the wild form."

Hydrangea japonica, Botanical Register, 30: t. 61, 1844. Lindley credited this name to Siebold and cited t. 53 of Siebold and Zuccarini's *Flora Japonica*. The Botanical Register plate shows a plant having an inflorescence in which the fertile flowers are rose colored and are surrounded by white sterile flowers. In flower color, therefore, it differs from Siebold and Zuccarini's plate in which the flowers are pink. The two probably represent color forms of *Hydrangea macrophylla* subsp. *macrophylla*.

Hydrangea japonica var. *caerulea*, Curtis's Botanical Magazine, t. 4253, 1846. This plate shows a plant having an inflorescence in which the fertile flowers are blue and the sterile flowers white. W. J. Hooker, who gave this blue-flowered plant the varietal name listed here, said that it is more handsome than the pink and rose flowered plants pictured in *Flora Japonica* and Botanical Register. It is undoubtedly a color form of *Hydrangea macrophylla* subsp. *macrophylla*.

Hydrangea Sitsitan Siebold, Nova Acta: Academia (caesarea) Leopoldino-Carolina, 692, 1829. Based on garden material, Siebold considered *Hydrangea Sitsitan* to be a dubious species, perhaps a form of his *H. hortensis*.

Hydrangea Thunbergii Siebold, l. c., 690. Siebold & Zuccarini, *Flora Japonica*, 1: 111, t. 58, 1839 or 1840. Siebold cited *Viburnum serratum* Thunberg as a synonym of his *Hydrangea Thunbergii* but said that because Thunberg's description was incomplete and imperfect he was not certain whether his plant was the same. He said further that the plant was known to him only in cultivation although it was said to grow in the provinces of Awa and Sanuki on Shikoku and in the mountains of Honshu. From the illustration it appears that this plant may be *H. macrophylla* subsp. *serrata*.

Hydrangea acuminata Siebold & Zuccarini, *Flora Japonica*, 1: 110, t. 56, 1839 or 1840. The illustration shows a plant with blue flowers. Like *H. Thunbergii*, it is difficult to tell from the illustration whether the plant represents *H. macrophylla* subsp. *serrata*. However, since it was said to grow in the mountains of Honshu and Kyushu it may represent *H. macrophylla* subsp. *serrata* rather than *H. macrophylla* subsp. *macrophylla*. Table 57 of the *Flora Japonica*, said also to represent *Hydrangea acuminata*,

shows a plant with capsules. The hypanthium of the capsule is somewhat abruptly constricted at the pedicel suggesting that the illustration should be referred to *H. scandens* subsp. *scandens* rather than *H. macrophylla* subsp. *serrata*.

Hydrangea Azisai Siebold & Zuccarini, *Flora Japonica*, 1:104, t. 51, 1839 or 1840. The plant illustrated has blue fertile flowers and several large pale blue sterile flowers, with some pubescence on the peduncles and pedicels. This name is based on a Japanese garden plant which Siebold and Zuccarini said was much sought after as an ornament in gardens and groves around temples. They said that it came originally from China and is so similar to the "Hortensia" that one can regard it as having had the same origin.

Hydrangea Belzonii Siebold & Zuccarini, *l. c.*, 109, t. 55. Siebold and Zuccarini described *Hydrangea Belzonii* as frequently cultivated in Japanese gardens, and having two forms, one with all sterile flowers and the other with both fertile and sterile flowers. The flowers in both are blue. They distinguished it from other garden forms of *Hydrangea macrophylla* subsp. *macrophylla* by its verticillate as well as opposite leaves.

Hydrangea Burgeri Siebold & Zuccarini, *l. c.*, 111, t. 57. This name was used by Siebold and Zuccarini for a Japanese garden plant with both sterile and fertile flowers. It appears from the illustration to be *H. macrophylla* subsp. *serrata*.

Hydrangea Otaksa Siebold & Zuccarini, *l. c.*, 105, t. 52. The illustration of *Hydrangea Otaksa* shows a plant with all sterile flowers and with leaves which appear to be thick in texture, as in *H. macrophylla* subsp. *macrophylla*. Siebold and Zuccarini considered this plant to strongly resemble Siebold's *H. hortensia* but preferred to keep it separate because of its obovate leaves and large clusters of blue flowers. It was, they said, rare in Japan and probably just recently imported from China. They also said that it was cultivated under the name of "Otaksa" in the botanical garden on the Isle of Deshima. It was on this small island in Nagasaki Bay that Thunberg and later Siebold stayed when they were in Japan and from whence came many of the plants which they both described.

Hydrangea stellata Siebold & Zuccarini, *l. c.*, 112, t. 59. *H. stellata* is described and illustrated as having mostly sterile flowers which are double and blue but not numerous. There is no clue as to which form this represents of *Hydrangea macrophylla*.

Hydrangea japonica rosalba Van Houtte, *Flore des Serres*, 16:75, tt. 1649, 1650, 1865-1867. Of the two illustrations representing *Hydrangea japonica rosalba* one has an inflorescence having white sterile flowers and the other an inflorescence with rose-colored sterile flowers. Both have numerous

white fertile flowers surrounded by the sterile flowers and thick appearing leaves which suggest *H. macrophylla* subsp. *macrophylla*.

Hydrangea Lindleyana Hort. ex Lavallée, Arboretum Segrezianum, 124, 1877. This horticultural name was doubtless applied to one of the garden forms of *H. macrophylla*. Lavallée lists it as a synonym of *H. Otaksa* Siebold & Zuccarini in his list of plants growing in the garden at Segrez in France.

Hydrangea sinensis Hort. ex Lavallée, *l. c.*, 123. Lavallée listed this horticultural name as a synonym under *H. japonica* Siebold & Zuccarini and doubtless it was one of the garden forms of *H. macrophylla* having both fertile and sterile flowers.

Hydrangea macrocephala Hort. ex Dippel, Handbuch der Laubholzkunde, 3: 322, 1893. This was a horticultural name published by Dippel as a synonym under his combination *Hydrangea opuloides* var. *a. Hortensia*. It was said to have a very large inflorescence and doubtless refers to a garden form of *H. macrophylla* having all sterile flowers.

Hydrangea mandschurica Hort. ex Dippel, *l. c.*

Hydrangea nigra Hort. ex Dippel, *l. c.*, 323. *Hydrangea mandschurica* and *H. nigra* were horticultural names which Dippel published as synonyms under his combination *H. opuloides* var. *cyanoclada*, which he described as having dark purple young shoots and rose-colored, mostly sterile flowers.

Hydrangea Sieboldii Hort. ex Dippel, *l. c.* Another horticultural name, this was published by Dippel under his combination *H. opuloides* var. *Hortensia* forma *macrosepala*, which he said had unusually large sterile flowers, and would doubtless be a garden form of *H. macrophylla*.

Section II. CORNIDIA

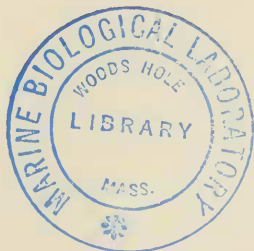
Section *Cornidia* (Ruiz & Pavón) Engler in Engler & Prantl, Natürlichen Pflanzenfamilien, 3, 2a, 76, 1891.

Cornidia Ruiz & Pavón, Flora Peruviana et Chilensis Prodrum, 53, t. 35, 1794, as genus.

Sarcostyles Presl ex Seringe in DeCandolle, Prodrum, 4:15, 1830, as genus.

Evergreen climbers, clinging by aerial rootlets, occasionally erect shrubs; leaves coriaceous; bracts few, broadly ovate, at base of inflorescence, enveloping the unopened inflorescence, leaving noticeable scars on falling; stamens 10; ovary inferior; capsule truncate at apex; seeds elliptical. Mexican, and Central and South American species, except *Hydrangea integrifolia* which is Philippine and Formosan.

Type species: *Hydrangea Preslii* Briquet (based on *Cornidia umbellata* Ruiz & Pavón).



Subsection 1. MONOSEGIA

Hydrangea, sect. Cornidia, subsect. Monosegia Briquet, Annuaire Conservatoire et Jardin Botaniques de Genève, 20:396, 1919.

Inflorescences consisting of single terminal cymes; flowers white or pink; sterile flowers present or absent.

TYPE SPECIES: *Hydrangea Preslii* Briquet.

12. *Hydrangea Seemannii* Riley, Kew Bulletin, 207. 1924.

Woody climbers; branchlets ferruginous pubescent with stellate hairs about 0.3 mm. long; leaves oval, 5–20 cm. long, 1.5–6 cm. wide, about 3 times as long as wide; upper surface glabrous, lower with few stellate hairs; margins entire; petioles 1–5 cm. long; inflorescence glabrous; flowers white; sterile flowers usually present; hypanthium 1.5 mm. long; calyx lobes 4 or 5, 0.2–0.3 mm. long; petals 4 or 5, 2 mm. long, 1 mm. wide; stamens 8 or 10, 2.8 mm. long; styles 2 or 3, 1 mm. long during anthesis, clavate; capsule 2.5 mm. long, 3.5 mm. wide, mature styles 1.5 mm. long.

DISTRIBUTION: Durango, Mexico, in the Sierra Madre Occidental, at approximate elevations of 2,000–2,600 meters.

TYPE LOCALITY: Mexico. Durango: "in barrancas climbing and rooting on old trees, like Ivy," at a locality in the Sierra Madre Occidental of Mexico called Rancho de Guadalupe between Mazatlan and Durango, at 6,000 feet. Type collection: *Seemann 2142* (holotype, K, isotype, BM).

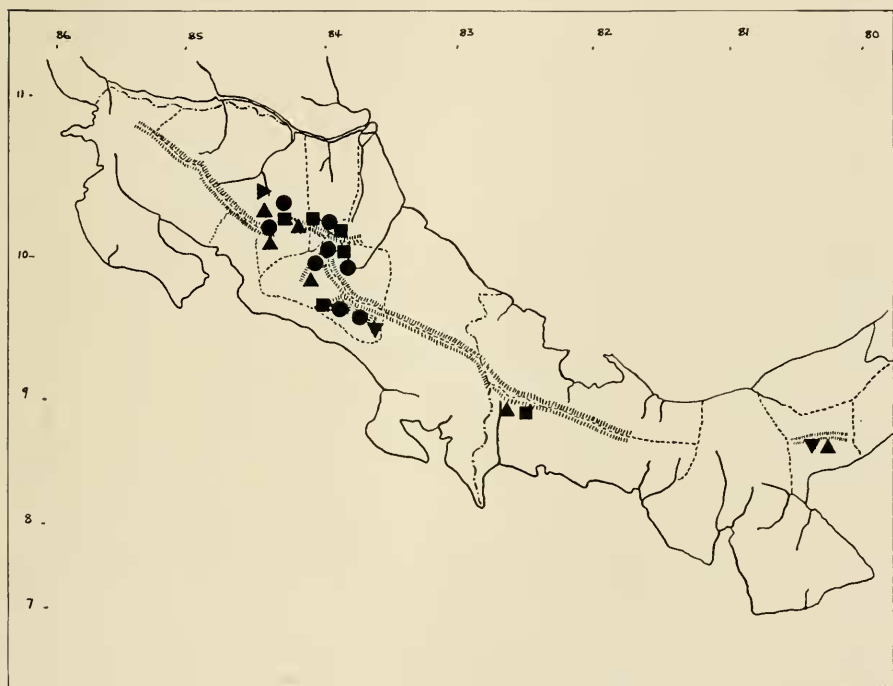
SPECIMENS EXAMINED: MEXICO. DURANGO: Sierra Madre. *Seemann 922* (K); about 35 miles west of El Salto, 2,400–2,500 m., *McVaugh 11536* (MICH, CAS); San Luis, 2,600 m., *Maysilles 7223* (MICH, CAS).

Hydrangea Seemannii is the only species of the genus known to occur in Mexico, where it has been found in the Sierra Madre Occidental between Mazatlan and Durango in the State of Durango. In flower *H. Seemannii* is readily recognized for it is one of two American species in the subsection Monosegia having white flowers. Its fruits, however, are indistinguishable from the pink-flowered *H. Oerstedii* and *H. peruviana*, and Seemann's specimen, a fruiting one with faded sterile flowers, was generally placed in one or the other of these species before *H. Seemannii* was created for it. *H. Seemannii* has been known only from the type specimen until the collections of McVaugh and Maysilles were made. The collection of Maysilles, a flowering one, has established the true relationship of this species.

13. *Hydrangea asterolasia* Diels, Notizblatt Königlicher Botanischer Garten und Botanisches Museum Berlin-Dahlem, 15: 370. 1941.

Hydrangea epiphytica Morton ex Haworth-Booth in M. Haworth-Booth, *The Hydrangeas*, p. 66, 1950. (Published without Latin diagnosis and without designation of a type specimen; however, *Sketch 3342* from Heredia, Costa Rica, was the basis of Morton's herbarium name.)

Woody climbers or shrubs; branchlets and inflorescence ferruginous tomentose with lax stellate hairs 0.5–0.8 mm. long; leaves oval, 5–10 cm. long, 3–5 cm. wide, 2–2.5 times as long as wide; upper surface glabrous; lower surface and petioles tomentose with gray or brown hairs; flowers white; sterile flowers usually present; hypanthium 1.5 mm. long; calyx lobes 4, 0.5 mm. long; petals 4, 1.5–2 mm. long; stamens 8, rarely 10, 3–4 mm. long; styles 2, 1–1.5 mm. long during anthesis, clavate; capsule 2 mm.



MAP 9. Distribution in Costa Rica and Panama of

- ▲ *Hydrangea Oerstedii*
- *Hydrangea asterolasia*
- *Hydrangea peruviana*
- ◄ *Hydrangea diplostemonia*
- ▼ *Hydrangea Preslii*

long, 2.5 mm. wide at apex; mature styles 2 mm. long; seeds striate, 1 mm. long. (See plate 4, figure 3.)

DISTRIBUTION: Mountains of central Costa Rica and Panama, Andes of Colombia and Ecuador, from 1,200 to 2,500 meters elevation. (See maps 9 and 10.)

TYPE LOCALITY: Ecuador. Napo-Pastaza, Mera. Type collection: *Schultze-Rhonhoff 2675* (destroyed, formerly B). No duplicate material of this collection has been located. Therefore, a topotype, *Lugo 49* (S), is here designated as the neotype.

SPECIMENS EXAMINED: COSTA RICA. SAN JOSÉ: La Palma de San Ramón, 1,200–1,300 m., *Brenes 3833* (F), *5265* (F), *5959* (F), *5226* (F); Las Nubes, 7,300 ft., *Lankester K248* (F, K); Santa María de Dota, 1,500 m., *Valerio 1359* (F); El Roble, *Stork 2029* (F); Irazú, *Lankester 1186* (F); Salitral de Desamparados, *Pittier 1157* (BM). HEREDIA: Vara Blanca de Sarapiquí between Poas and Barba volcanos, *Skutch 3342* (type collection of *H. epiphytica*, holotype US, isotypes A, MO, K, NY), *3339* (MO, A, K, NY). GUANACASTE: Palmira, 6,000 ft., *Smith A502* (A, F, NY). ALAJUELA: Tapisco, 1,700 m., *Smith 2745* (MO, F); region of Zarcerro, *Smith H470* (MO, F), *1281* (NY). PANAMA. CHIRIQUÍ: Boquete district, *Davidson 74* in part (A). COLOMBIA. ANTIOQUIA: Yarumál, *Bro. Tomás 1618* (US). Without precise locality: *Mutis 3670* (US). A specimen consisting of a leaf only (*García-Barriga 4896*, US) collected at Yamara, intendancy of Meta, Colombia, may belong here. ECUADOR. NAPO PASTAZA: Mera, *Lugo 49* (S, selected as a neotype).

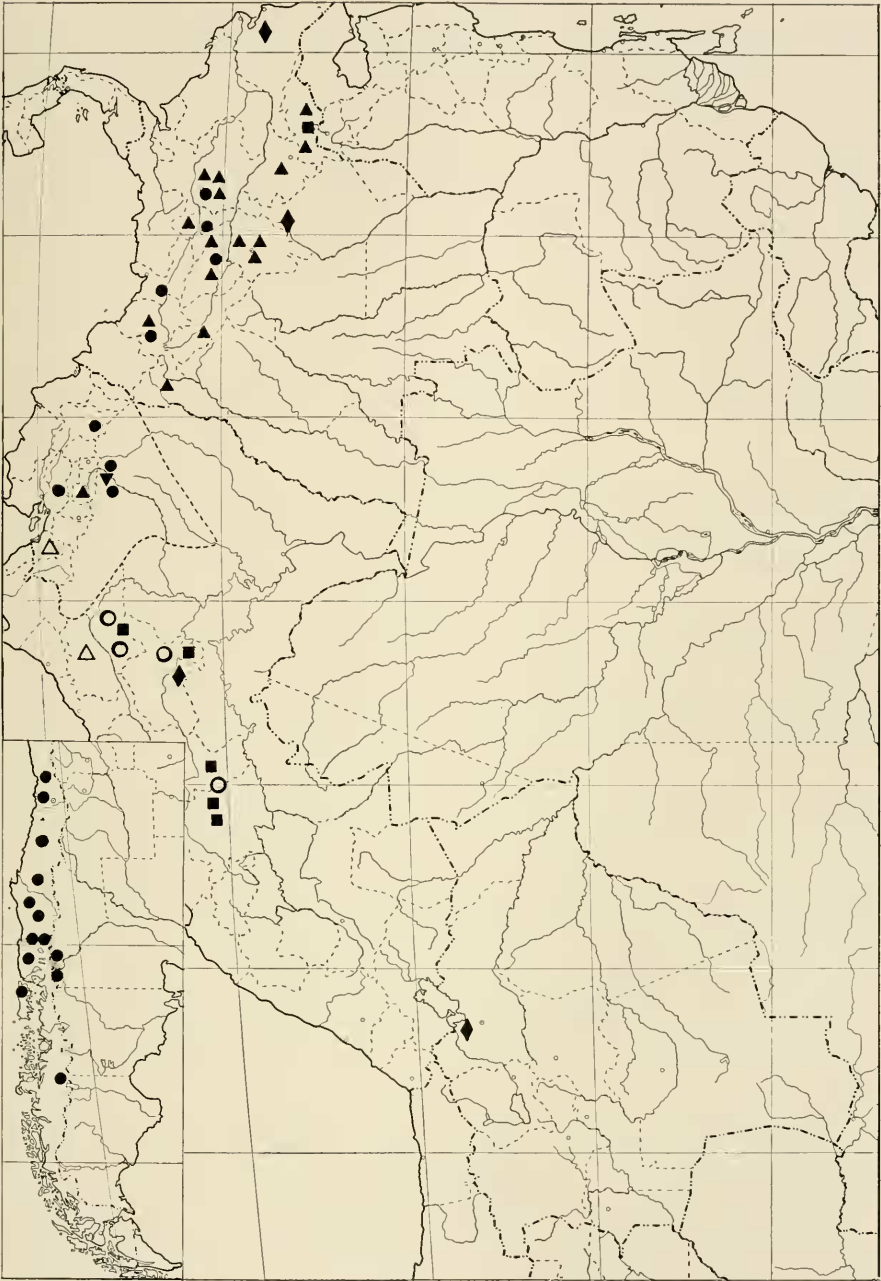
Hydrangea asterolasia is distinguished from the other species in subsec-

MAP 10. Distribution in the northern Andes of

- ▲ *Hydrangea Oestedi*
- ▼ *Hydrangea asterolasia*
- *Hydrangea peruviana*
- *Hydrangea diplostemonia*
- *Hydrangea Preslii*
- ◆ *Hydrangea tarapotensis*
- ✚ *Hydrangea Mathewsii*
- △ *Hydrangea Jelskii*

Inset: Distribution in Chile of

- *Hydrangea serratifolia*



tion Monosegia by the combination of its white flowers, its pubescence, and its leaf size. The pubescence, consisting of a ferruginous or grayish, stellate tomentum is similar to that seen in *H. Matheursii* and *H. Jelskii*, both of subsection Polysegia. The leaves of *H. asterolasia* are generally smaller than those of the other species in this subsection. All of the specimens examined of this species had two styles which were always shorter than the stamens. The styles develop their stigmatic papillae during the bud stage and by early anthesis they are clavate and have a conspicuous stigmatic surface.

14. **Hydrangea integrifolia** Hayata, Journal College of Science, Imperial University, Tokyo, 22: 131. 1906.

Hydrangea integra Hayata, Journal College of Science, Imperial University, Tokyo, 25(19):90. 1908. Type from Formosa, *Kawakami & Mori 1723*.

Hydrangea glandulosa Elmer, Leaflets Philippine Botany, 2:473. 1908. Type from Negros Island, Philippine Islands, *Elmer 9846*.

Hydrangea cuneatifolia Elmer, l. c. 8:2825. 1915. Type from Sibuyan Island, Philippine Islands, *Elmer 10732*.

Woody climbers or shrubs, pubescence on inflorescence of coarse stellate hairs (0.15–0.25 mm. long) borne on short (0.05 mm. long) epidermal papillae, pubescence on stem dense, of fine stellate hairs with occasionally coarser hairs interspersed; leaves oval, 5–18 cm. long, 3–9 cm. wide, 1.5 to 3.5 times as long as wide; margins entire to remotely denticulate; upper surface glabrous; lower surface mostly glabrous except for occasional scattered coarse hairs and clusters of fine hairs in the axils of the secondary veins; flowers white; sterile flowers present; hypanthium 0.8–1.3 mm. long; calyx lobes 4 or 5, 0.2–0.3 mm. long; petals 4 or 5, 1.4–2.2 mm. long; stamens 8–10, 1.5–4 mm. long; styles two or three, 0.8–1.2 mm. long during anthesis, clavate; capsules 1.5–2.5 mm. long, fruiting styles 1.5–2 mm. long. (See plate 4, figure 9.)

DISTRIBUTION: Philippine Islands and Formosa.

TYPE LOCALITY: Formosa. Taito-cho: Taito. Type collection: *Faurie 105* (holotype TI, isotype BM).

ILLUSTRATIONS:

B. Hayata, 1908. Flora Montana Formosae in Journal College of Science, Imperial University, Tokyo, 25(19): plate 7, as *H. integra*.

SPECIMENS EXAMINED: FORMOSA. TAINAN-SHU: Arisan, 1,000–2,800 m., *Wilson 9691* (A, US), *1082* (A), *Keng 1095* (US), *Faurie 143* (A, G, BM), *144* (G, BM), *Kunehira 2841* (NY, US). TAICHU-SHU: Niitaka-yama (Mt. Morrison), *Kawakami & Mori 1723* (type collection of *Hydrangea integra* (holotype TI, photo A); Mt. Nanko, 7,000–8,000 ft., *Sasaki W268* (A).

PHILIPPINE ISLANDS. LUZON ISLAND: Mountain Province: Ifugao Subprovince, Mt. Polis, *McGregor in 1913* (UC, P, US), *Celastino in 1948* (A); Benguet Subprovince, Mt. Mangaoto, *Quisumbing & Sulit 6374* (NY), Pauai, *Merrill 4771* (K), *Santos in 1918* (UC, P, K, A); Bontoc Subprovince, Mt. Pukis, *Ramos & Edaña in 1920* (US, P, K). Rizal Province: *Loher in 1913* (UC, A), Batay, *Loher 5992*, in 1905 (K), Mt. Anilog *Ramos in 1922* (A, P, K, US), Montalban, *Loher 13179* (UC, P). LAGUNA PROVINCE: Mt. Cristobal, *Sulit et al. in 1927* (NY, UC), *Juliano 1082* (UC), *Canicosa in 1922* (A, P, K, US). LEYTE ISLAND: Dagami, *Ramos in 1912* (US, P, K). SIBUYAN ISLAND: Mt. Guitingitau, *Elmer 10732* (type collection of *Hydrangea cuneatifolia*, isotypes NY, E, G, GH, K, A). NEGROS ISLAND: Negros Oriental Province: Cuernos de Negros near Dumaguete, *Elmer 9846* (type collection of *Hydrangea glandulosa*, isotypes NY, E, G, GH, P, K, A). MINDANAO ISLAND: Cotabato Province: Mt. Apo, *Clemens in 1924* (NY, P, UC).

Hydrangea integrifolia is the only species of the section Cornidia found in the Old World, where it occurs in Formosa and the Philippine Islands. The character of its inflorescence, consisting of a single terminal cyme, places it in the subsection Monosegia. It is further characterized by having both sterile and fertile flowers which are white, and fertile flowers which have 4 or 5 sepals and petals and 8 or 10 stamens. These characters are also found in *H. Seemannii*, so that even though *H. Seemannii* and *H. integrifolia* are widely separated geographically, they resemble each other very closely.

15. **Hydrangea Oerstedii** Briquet, *Annuaire Conservatoire et Jardin Botaniques de Genève* 20: 407. 1919. Based on *Cornidia radiata* Oersted.

Cornidia radiata Oersted, *Dansk. Naturhist. For. Kjoebenhavn, Vidensk. Meddel.*, 42. 1856. Non *Hydrangea radiata* Walter, *Flora Caroliniana* 251. 1788.

Hydrangea durifolia Briquet, *Annuaire Conservatoire et Jardin Botaniques de Genève*, 20: 406. 1919. Type from Norte de Santander, Colombia, *Funk & Schlim 1393*.

Hydrangea Schlimii Briquet, *l. c.* 400. Type from Norte de Santander, Colombia, *Linden 1139*.

Hydrangea Goudotii Briquet, *l. c.*, 404. Type from Caldas, Colombia, *Goudot s. n.*

Hydrangea platyphylla Briquet, *l. c.*, 401. Type from Tolima, Colombia, *Linden 894*.

Woody climbers or shrubs; branchlets and inflorescence pubescent with erect, single or stellate hairs 0.1–0.3 mm. long, or occasionally additional longer, simple ones; leaves oval, 10–21 cm. long, 4–9 cm. wide, about 1.5 times as long as wide; pubescence on lower surface similar to that of the inflorescence; upper surface glabrous; margins remotely denticulate to nearly entire; petiole 1–3 cm. long; flowers pink; sterile flowers present;

hypanthium 1–1.5 mm. long; calyx-lobes 4, 0.5 mm. long; petals 4, 1–2 mm. long, 1 mm. wide; stamens 8, 2–4.5 mm. long; styles 2, rarely 3, 0.3–1 mm. long, slender, acute at apex, the stigmatic surface inconspicuous during anthesis; capsule 2 mm. long, 2.5 mm. wide at apex, the mature styles 2 mm. long, with conspicuous stigmatic surface; seeds linear, striate, 0.5 mm. long.

DISTRIBUTION: Mountains of Central Costa Rica and Panama, and the Andes of Colombia, Ecuador and Peru, from 1,300 to 3,000 meters elevation. (See maps 9 and 10.)

TYPE LOCALITY: Costa Rica, San José: Candelaria. Type collection of *Cornidia radiata*: Oersted 1782 (holotype C, isotypes, C, US, K, F).

SPECIMENS EXAMINED: COSTA RICA. SAN JOSÉ: Candelaria, Oersted Feb. 1847 (C, US). ALAJUELA: Fraijanes, 1,500–1,700 m., Standley & Torres 47755 (US). CARTAGO: Tapanti, 1,300 m., Valerio 1658 (F). Localities uncertain or not precisely stated: Warscewicz s. n. (fragment G, photo F); Hubsch in 1887 (K); San Carlos de Ramón, Endres 505 (W). The following fruiting specimens from Costa Rica may belong to this species: ALAJUELA: region of Zarcero, Smith A737; La Palma de San Ramón, Brenes 6736, Tonduz 12507. CARTAGO: Friedrichsthal 1431 (W). SAN JOSÉ: La Hondura, Standley 36583, 37781; Santa María de Dota, Standley & Valerio 44125. PANAMA. CHIRIQUÍ: Rio Chiriquí Viejo, 1,800–2,000 m., Allen 1400 (MO, GH, US); Baja Mono and Quebrada Chiquero, 1,500 m., Woodson & Schery 511 (MO, GH, US). COCLÉ: El Valle de Antón, 1,000 m., Allen 2693 (MO, US). COLOMBIA. ANTIOQUIA: Yarumál, Jervise s. n. (K); Nariño, en la quebradito de El Oso, 1,900 m., Uribe 1913; San José de San Andrés, Correa & Velasquez 45, (US, MEDEL). CALDAS: San Félix, Bro. Tomás 1859 (US); "massif du Quindío á Portiobulla," Goudot s. n. (type collection of *Hydrangea Goudotii*, holotype G); Manizales, Triana s. n. (K). CUNDIAMARCA: Zipaquirá, Huertas & Camargo 32a (F); Sasaima, García-Barriga 12556 (US); Bogotá, Holton 661 (PH, K). CAUCA: San José, Pennell 7607 (PH, GH, NY). HUILA: La Plata, Sneidern 2811 (S). Norte de Santander: Pamplona, Funck & Schlim 1393 (type collection of *Hydrangea durifolia*, holotype G, fragment and photo F); Culagá Valley, 1,500–2,100 m., Killip & Smith 20477 (US, GH, A, NY); Ocaño, Linden 1139 (type collection of *H. Schlimii*, holotype G). SANTANDER: La Baja, 3,000 m., Killip & Smith 18366 (A, GH, US); Las Vegas, 2,600–3,000 m., Killip & Smith 16079 (US, GH, A), 16089 (US, S, F, GH, A, BM, NY). PUTUMAYO: La Cabaña, 2,800 m., Cuatrecasas 11639 (US, F). TOLIMA: Ibaqué, Goudot s. n. (G, W.); Mariquita, Linden 894 (type collection of *Hydrangea platyphylla*, holotype G, isotypes K, W, fragment and photo F, photos US, A, NY). VALLE: Almorzadero, 2,980 m., Cuatrecasas 18113 (F). Localities uncertain or not precisely stated: Com-

bayma, *Goudot s. n.* (G), *Triana 358* (P, in part US); *Triana 359* (US, P, K); *Triana s. n.* (MICH, G); *Mutis 3667* (US, K, S, G), *3668*, (US), *3671* (US); *Linden 768* (W). ECUADOR. CHIMBORAZO: Mt. Chimborazo, 3,000 m., *Spruce s. n.* (K). LOJA: Tambo Cachijacu, *Steyermark 54751* (US, F, NY). PICHINCHA: Oya Cachi, *Acosta-Solis 11144* (F). PERU. SAN MARTÍN: Río Almirante, *Sandeman 168* (K).

Hydrangea Oerstedii has been said by Standley (*Flora of Costa Rica* in Field Museum of Natural History—Botany 28:474. 1937) to be “a scandent shrub, climbing over tall trees, or sometimes an erect shrub or tree” and to be “one of the most beautiful plants of Costa Rica because of its broad cymes of showy flowers, which are not inferior in beauty to those of cultivated species.” The cymes are composed of pink fertile and sterile flowers. The fertile ones are small but numerous, and are surrounded by the larger, more conspicuous sterile ones.

Hydrangea Oerstedii is the only species in the subsection *Monosegia* in which the styles are always shorter than the stamens. During early anthesis, they are less than 1 mm. long, attenuate toward the apex and without evident stigmatic papillae. Sometime during late anthesis, they become longer and stigmatic papillae begin to develop, and at maturity they are thickened at the apex and have a conspicuous stigmatic surface. The latent development of the stigmatic surface, known only in this species of subsection *Monosegia*, occurs also in *H. serratifolia* in subsection *Polysegia*.

Hydrangea Oerstedii is very closely related to *H. peruviana*. A discussion of this relationship will be found under *H. peruviana*.

16. ***Hydrangea peruviana*** Moricand, in DeCandolle, *Prodromus*, 4:14. 1830.

Cornidia peruviana (Moricand) Small, *North American Flora*, 22:161. 1905.

Hydrangea Trianae Briquet, *Annuaire Conservatoire et Jardin Botaniques de Genève*, 20:403. 1919. Type from Tolima, Colombia, *Triana in 1851–1857*.

Hydrangea panamensis Standley, *Journal Washington Academy Science*, 17:10. 1927. Type from Colón, Panama, *Pittier 3919*.

Hydrangea Weberbaueri Engler, in Engler and Prantl, *Natürlichen Pflanzenfamilien*, ed. 2, 18a:207. 1930. Type from Amazonas, Peru, *Weberbauer 3272*.

Hydrangea caucana Engler, *l. c.* 206. Type from Cauca, Colombia, *Lehmann 5106*.

Hydrangea Lehmannii Engler, *l. c.* 207. Type from Andes near Cali, Colombia, *Lehmann 9074*.

Woody climbers or shrubs; branchlets and inflorescence pubescent with erect, stellate hairs 0.3–0.5 mm. long, older portions of stem covered with coarse, linear trichomes; leaves oval, 10–25 cm. long, 5–15 cm. wide, 2–3 times as long as wide, both surfaces glabrous or occasionally pubescent,

margins entire to remotely denticulate; flowers pink; sterile flowers present; hypanthium 1.5 mm. long; calyx-lobes 4, 0.4 mm. long; petals 4, 1.5 mm. long, 1 mm. wide; stamens 8, 0.4–1.6 mm. long; filaments shorter than styles; styles 2, rarely 3, 1–2 mm. long during anthesis, clavate; capsule 2 mm. long, 2.5 mm. wide at apex, mature styles 2 mm. long. (See plate 4, figure 4.)

DISTRIBUTION: Mountains of central Costa Rica and Panama, Andes of Colombia, Ecuador and Peru, from 1,200 to 3,200 meters elevation. (See maps 9 and 10.)

ILLUSTRATION:

Saxifragaceae in Flora of Panama, Annals of the Missouri Botanical Garden, 37: 141. 1950.

TYPE LOCALITY: Ecuador. Guayas: Guayaquil. Type collection: *Parón s. n.* (holotype G, photo F).

SPECIMENS EXAMINED: COSTA RICA. ALAJUELA: La Peña de Zarcero, 4,000 ft., *Smith 1685* (F, MO); La Palma de San Ramón, 1,200–1,300 m., *Brenes 3807* (F), *5163* (F), *3984* (F). CARTAGO: Alto de la Estrella, *Standley 39080* (US). HEREDIA: Vara Blanca de Sarapiquí, between Poas and Barba Volcanos, 1,680 m., *Skutch 3393* (US, K, S, MO). SAN JOSÉ: La Palma, 1,600 m., *Standley 33163* (US, A); Tablazo, 1,800 m., *Valerio 1247* (F); near Finca La Cima, north of El Copey, 2,100–2,400 m., *Standley 42569* (US); San Isidro de Coronada, *Allen 534* (A, F); La Hondura, 1,300–1,700 m., *Standley 36249* (US). PANAMA. COLÓN: along Río Fato, 10–100 m., *Pittier 3919* (type collection of *Hydrangea panamensis*, holotype US, isotypes NY, GH, C, A, BM, F). CHIRIQUÍ: Bajo Chorro, Boquete district, 6,000 ft., *Davidson 74* in part (MO, F, US); Valley of the upper Río Chiriquí Viejo, *White 90a* (MO). COCLÉ: El Valle de Antón, 1,000 m., *Allen 3712* (US, G, E, F). COLOMBIA. ANTIOQUIA: La Ceja, 3,200 m., *André 2186* (K, F, US); Santa Elena, 2,300–2,500 m., *Medina 239* (MEDEL). CALDAS: La Selva, 1,600–1,900 m., *Sneidern 5265* (CAS, F); Manizales, *Triana s. n.* (BM). CAUCA: Aguabonita, 2,280 m., *Cuatrecasas 23547* (F). Cimarronas, 1,200–1,600 m., *Lehmann 5106* (type collection of *Hydrangea caucana*, isotypes F, K); El Tambo, *Sneidern 628* (F, S), *817* (S), *1402* (S). TOLIMA: Quindío, *Triana in 1851–1857* (type collection of *Hydrangea Trianae*, type G, photo and fragment F). VALLE: Piedra de Moler, 900–1,180 m., *Cuatrecasas 14974* (F); between Quermal and La Elsa, 1,160–1,200 m., *Cuatrecasas 23994* (F); La Elsa, 1,000–1,200 m., *Cuatrecasas 15326* (F); between Los Carpatos and El Olivo, 2,025–2,920 m., *Cuatrecasas 21935* (F); Cali, *Lehmann B. T. 623* (NY, K), *9074* (type collection of *Hydrangea Lehmannii*, isotype K), *2929* (G). Without precise locality: *Bro. Ariste-Joseph 820A* (US); *Purdie in 1825* (K); *Triana 358*

in part (K); *Lobb s.n.* (K); *Pérez-Arbelácz 3072* (US). ECUADOR. NAPO-PASTAZA: Mera, *Lugo 126* (fruiting specimen, determination not certain, S); valley of Rio Papallaeta, *Asplund 8782* (S). CHIMBORAZO: Canelos, *Spruce 5380* (K, W). PICHINCHA: *Karsten s. n.* (W); Quito, *Jameson s. n.* (K), 586 (E). Without precise locality: *Heinrichs 741* (G, NY). PERU. AMAZONAS: Cheto, *Weberbauer 3272* (type collection of *Hydrangea Weberbaueri*, isotype G, photo and fragment F). Without precise locality: *Pavon s. n.* (P).

Hydrangea peruviana has the same showy inflorescences which are seen in *H. Oerstedii*. So close are these two species to each other that they can be distinguished only by the relative length of the stamens and styles of the two. In *H. Oerstedii* the styles are always shorter than the stamens and the styles develop their stigmatic surfaces during anthesis, while in *H. peruviana* the styles are the same length as, or longer than, the stamens, and the styles develop their stigmatic surfaces during the bud stages. The stamens in *H. Oerstedii*, besides being longer than the styles, have well developed anther sacs, which, in most of the stamens examined, were full of pollen. However, in *H. peruviana*, the stamens, which scarcely exceed the styles, have small and undeveloped anther sacs which contained no pollen in any of the specimens examined. The close morphological resemblance and the overlapping geographic distribution of these two species, together with the undeveloped anthers of *H. peruviana* and the latent development of the style of *H. Oerstedii*, suggest that the two may represent the two forms of a dimorphic species.

17. *Hydrangea diplostemonia* (Donnell Smith) Standley, Journal Washington Academy of Science, 18:160. 1928.

Gilibertia diplostemonia Donnell Smith, Botanical Gazette, 61:373. 1916.

Hydrangea Sprucei Briquet, Annuaire Conservatoire et Jardin Botaniques de Genève, 20:412. 1919. Type from San Martín, Peru, *Spruce 4328*.

Hydrangea inornata Standley, Journal Washington Academy of Science, 17:9. 1927. Type from Cartago, Costa Rica, *Pittier 14068*.

Woody climbers or shrubs; branchlets and inflorescence pubescent with stellate hairs 0.3–0.5 mm. long, or occasionally longer, lax, simple hairs; leaves oval, 15–25 cm. long, 5–15 cm. wide, 2–3 times as long as wide; upper surface glabrous; lower surface occasionally pubescent; margins entire; petiole 1.5–2.5 cm. long; flowers pink; sterile flowers usually absent; hypanthium 1–1.5 mm. long; calyx-lobes 4, 0.5 mm. long; petals 4, 1.5–2 mm. long; stamens 8, rarely 10, 2–3 mm. long; styles 2 or 3, 1–1.5 mm. long, coherent in bud, more or less spreading to completely separate in anthesis; mature fruits not seen. (See plate 4, figure 7.)

DISTRIBUTION: Mountains of central Costa Rica, and northern Andes, from 600 to 1,500 meters elevation. (See maps 9 and 10.)

TYPE LOCALITY: Costa Rica. Cartago: forests of Tuís. Type collection of *Gilbertia diplostemonia*: Pittier 14068 (holotype US, Herb. No. 1417096).

SPECIMENS EXAMINED: COSTA RICA. ALAJUELA: San Carlos, 1,025 m., Smith II1643 (A, F, MO). CARTAGO: forests of Tuís, 700 m., Pittier 14068 (holotype of *Hydrangea inornata*, US, Herb. No. 577962); Irazú volcano, near Guayabillos, Cufodonti 392 (G). COLOMBIA. TOLIMA: Quindío, Linden 1097 (G). PERU. Huánuco: Río Pozuzo, 1,300–1,400 m., Weberbauer 6744 (US, GH, F); Pampayacu, Savada P44 (F). SAN MARTÍN: Tarapoto, Spruce 4328 (type collection of *Hydrangea Sprucei*, holotype G, isotypes E, C, GH, W, K.)

Hydrangea diplostemonia is a poorly defined entity, being characterized chiefly by its coherent styles. The styles, coherent during the bud stages, separate sometime during anthesis. The styles, when separate, have a conspicuous stigmatic surface and are shorter than the stamens. The anthers always appear well developed. Sterile flowers are usually absent, although two specimens have them, Smith II1643 and Cufodonti 392. The Geneva specimen of Cufodonti 392 is in anthesis but has only a few flowers with the styles united. The Vienna specimen of this collection has young fruits and, because it has sterile flowers, it appears to be like *H. Oerstedii*.

The collection of Spruce 4328, without sterile flowers, is represented in several European herbaria. The specimen at Geneva is one of two collections cited by Briquet under his *H. Sprucei*. He did not designate either as the type, but since he named his species for Richard Spruce, the specimen collected by Spruce should, or doubtlessly may, be considered to be the type. The other specimen, Schlim 1140, belongs to *H. Preslii*. The Geneva specimen of Spruce 4328, partly in bud and partly in anthesis, has coherent styles in the buds; in anthesis the styles are separate. Of the three sheets at Kew, the flowers in bud and in anthesis have the same condition of the style as the Geneva specimen; however, an inflorescence with flowers in late anthesis has the styles separate, without a trace of being coherent, and the inflorescence appears to be like that of *H. Preslii*. A specimen in the British Museum of Natural History has fairly well developed capsules, and also appears to be like *H. Preslii*.

18. ***Hydrangea Preslii*** Briquet, *Annuaire Conservatoire et Jardin Botaniques de Genève* 20:409. 1919. (Based on *Sarcostyles peruviana* Presl 1830.)

Cornidia umbellata Ruiz & Pavón, *Systema Vegetabilium*, 91. 1798. Type from Peru, Pavón, s. n.

Sarcostyles peruviana Presl in DeCandolle, Prodrumus, 4:16. 1830. Non *Hydrangea peruviana* Moricand in DeCandolle, Prodrumus, 4:14. 1830.

Hydrangea umbellata (Ruiz & Pavón) Briquet, Annuaire Conservatoire et Jardin Botaniques de Genève, 20:411. 1919. Non *Hydrangea umbellata* Rehder, Plantae Wilsonianae, 1:25. 1911. Based on *Cornidia umbellata* Ruiz & Pavón.

Hydrangea ecuadorensis Briquet, l. c., 410. Type from Tungurahua, Ecuador, Spruce 5058.

Hydrangea Briquetii Engler in Engler and Prantl, Natürlichen Pflanzenfamilien, 18a: 207, ed. 2. 1930. Based on *Hydrangea umbellata* (Ruiz & Pavón) Briquet.

Woody climbers or shrubs; branchlets and inflorescence pubescent with single or stellate hairs, 0.1–0.2 mm. long; leaves oval, 9–20 cm. long, 2–10 cm. wide, 2–3 times as long as wide, margins entire; petiole 15–20 mm. long; flowers pink; sterile flowers absent; hypanthium 1.5 mm. long, calyxlobes 4, 0.5 mm. long; petals 4, 1.5–2 mm. long, 1 mm. wide; stamens 8, 1.5–3 mm. long; styles usually 3, occasionally 4, 1–1.5 mm. long, occasionally thickened at base; capsule 2 mm. long, 2.5 mm. wide at apex, mature styles 1.5–2 mm. long. (See plate 4, figure 6.)

DISTRIBUTION: Mountains of central Costa Rica and Panama, Andes of Colombia, Ecuador and Peru, from 1,000 to 2,500 meters elevation. (See maps 9 and 10.)

TYPE LOCALITY of *Sarcostyles peruviana* Presl: Peru. Type collection: *Haenke s. n.* (isotype MO).

SPECIMENS EXAMINED: COSTA RICA. SAN JOSÉ: El General, 1,100 m., *Skutch 2630* (A, NY, S, MO, K, MICH), *2538* (A, S, NY, K, MO). PANAMA. COCLÉ: La Mesa, 1,000 m., *Allen 2332* (US). COLOMBIA. NORTE DE SANTANDER: Pamplona, *Schlim 1140* (G). ECUADOR. TUNGURAHUA: Baños, *Spruce 5058* (type collection of *Hydrangea ecuadorensis*, holotype G, isotypes E, BM, K, W). PERU. AMAZONAS: Molinopampa, 2,400 m., *Weberbauer 4385* (fragment F). HUÁNUCO: Muña, *Macbride 3692* (F, US), *Pearce 183* (K); Rio Pozuzo, *Weberbauer 6776* (US, GH, F). JUNÍN: San Ramón, 1,300–1,700 m., *Schunke A36* (US, F); Huacapistana, *Sandeman 4455* (K). SAN MARTÍN: Zepelacio, 1,100–1,800 m., *Klug 3653* (MO, US, BM, K, NY, A, GH, CAS, S, F); Tarapoto, *Spruce 4452* (K). Without precise locality: *Haenke 109* (W, may be an isotype of *Sarcostyles peruviana*).

Hydrangea Preslii is the only species in the subsection Monosegia which always lacks sterile flowers. The styles are usually three, but sometimes there are two or four. The styles have a conspicuous stigmatic surface in the bud and anthesis stages. The length of the stamens is somewhat variable in relation to the style; they may be approximately the same length as the styles to as much as three times their length.

The relationship of this species to *H. diplostemonia* has been discussed under this species.

19. **Hydrangea Steyermarkii** Standley, Field Museum Publications, Botany, 22: 233. 1940.

Woody climbers, branchlets and inflorescence ferruginous tomentose with lax, stellate hairs about 0.5 mm. long; older portions of stem covered with coarse linear trichomes; leaves obovate to oblong, broadest above middle, 6.5–16 cm. long, 4–9 cm. wide, petioles 1–2.5 cm. long; flower color not known; sterile flowers absent; calyx lobes 5, occasionally 4, 1–2 mm. long, deltoid to semi-orbicular, variable in shape and size on individual flowers; petals not seen; stamens not seen; styles 2; capsule 2.5 mm. long, 3 mm. in diameter at apex, fruiting styles 1–2 mm. long.

DISTRIBUTION: Central Guatemala, from 1,500 to 3,000 meters elevation.

TYPE LOCALITY: Guatemala. San Marcos: along Quebrada Canjulá between Sibinal and Canjulá, Volcán Tacaná, 2,200–2,500 m. Type collection, *Steyermark 36044* (type F).

SPECIMENS EXAMINED (sterile or juvenile specimens only): GUATEMALA. SAN MARCOS: between Canjulá and La Unión Juárez, near south-east portion of Volcán Tacaná, 2,000–3,000 m., *Steyermark 3641*; between Tajumulco and Tecutla, northwestern slopes of Volcán Tajumulco, 1,800–2,500 m., *Steyermark 36812*; Baranca Eminencia, between San Marcos and San Rafael Pie de la Cuesta, 2,500–2,700 m., *Standley 86500, 86454, 86408*. QUEZALTENANGO: western slopes of Volcán Zunil, 1,500 m., *Steyermark 35109*. EL PROGRESO: between Finca Piamonte and top of Montaña Piamonte, along Joya Pacayul, 2,500–3,000 m., *Steyermark 43635*. ALTA VERAPAZ: mountains along road between Taatic and the divide on road to Tamohu 1,500–1,600 m., *Standley 91325*. SUCHITEPÉQUEZ: Volcán Santa Clara, *Steyermark 46680*. HUEHUETENANGO: wet cloud forest at Cruz de Limón, *Steyermark 49826*; Cerro Huitz, *Steyermark 48536*.

Hydrangea Steyermarkii is the only species of the genus found in Guatemala. The type specimen, the only fertile specimen seen, is in fruit; the flowers are not known. A number of sterile or juvenile specimens from Guatemala and which doubtless belong to this species, give some idea of its distribution.

Subsection 2. POLYSEGIA

Hydrangea, sect. Cornidia, subsect. Polysegia Briquet, Annuaire Conservatoire et Jardin Botaniques de Genève, 20:396, 1919.

Inflorescences consisting of a series of cymes, one above another, rarely of a single terminal cyme. Flowers white; sterile flowers always absent.

TYPE SPECIES: *Hydrangea serratifolia* (Hooker & Arnott) Philippi f.

20. ***Hydrangea serratifolia*** (Hooker & Arnott) Philippi f., *Plantarum Vascularium Chilensium* 97. 1881.

Hydrangea scandens Poeppig, in DeCandolle, *Prodromus*, 4:666. 1830. *Non Hydrangea scandens* (L. f.) Seringe in DeCandolle, *Prodromus*, 4:15. 1830. *Nec Hydrangea scandens* Maximowicz, *Mémoires Académie Impériale des Sciences de St. Pétersbourg*, Series 7, 10 (16):16. 1867. Type from Chile, *Poeppig in 1829*.

Cornidia integerrima Hooker & Arnott, *Botanical Miscellany*, 3:344. 1833. Two syntypes from Chile: Valparaíso, *Cuming 398*; Ñuble, *Bridges 532*.

Cornidia serratifolia Hooker & Arnott, *l. c.*

Hydrangea integerrima (Hooker & Arnott) Engler, in Engler and Prantl, *Natürlichen Pflanzenfamilien*, 3(2a):76, ed. 1, 1891.

Woody climbers or shrubs; young branchlets, leaves, and inflorescence pubescent with erect, stellate hairs, or occasionally additional longer, simple hairs; leaves oval, 7–14 cm. long, 3–5 cm. wide, 2–3 times as long as wide, margins entire or remotely serrate; both surfaces glabrous, lower often with scattered punctations and pockets along midrib (perhaps caused by an insect); flowers white, all fertile; hypanthium 1.5–2 mm. long; calyxlobes 4, acute to broadly ovate, 0.2–0.5 mm. long; petals 4, 2–2.5 mm. long; stamens 8, rarely 10, 3–7 mm. long; styles 3, occasionally 2 or 4, 0.5–1 mm. long during anthesis, acute at apex; capsules 2.5–3 mm. long; fruiting styles 2–2.5 mm. long, clavate. (See plate 4, figure 10.)

DISTRIBUTION: Central Chile and adjacent Argentina, about 800–1,500 meters elevation. (See Map 10, inset).

TYPE LOCALITY: Chile. Chiloé: Island of Chiloé. Type collection: *Cuming 34* (holotype K, isotypes G, BM, E).

ILLUSTRATIONS:

Curtis's Botanical Magazine, new series, table 153, 1951, as *H. integerrima*.

SPECIMENS EXAMINED: ARGENTINA. Río NEGRO: Puerto Blest, Lake Nahuel Hualpi, *Burkhardt 6361* (F), *Cordoni 6* (US), *Parodi 11797* (GH), *11795* (GH). CHUBUT: Lago Menendez, Cerro Torrecillos, *Castellanos 117650* (Feb. 2, 1945) (G). CHILE. ACONCAGUA: Valle de Marga-Marga, *Jaffuel & Pirion 3282* (GH), *Jaffuel 242* (GH). AYSÉN: *Dusen January 1897* (O); Puerto Aysén, *Pirion 3472* (GH), *Looser 4805* (GH). BIO BIO: Pailahueque, *Pirion 195* (GH); Antuco, *Poeppig 760* (BM, W). CAUTÍN: Cunco, *Clavde-Joseph 18050* (UC); Maquehue, *Morton in 1906* (G, BM); Temuco, *Bro. Claude-Joseph 4676* (US), *Sargent in 1906* (MO, A), *Elliott 592* (E, GH, K); Río Cautín, *Hollermeyer in 1919* (G). CHILOÉ: Piruquina, *Junge*

112 (MO); Island of Chiloé, *Capt. King* (collected during voyage of the *Adventure* 1826-30) (BM, K), *Skottsberg* 373 (S). CURICÓ: *Werderman* (G, F, US, NY, CAS, MO, UC, E, K, S, GH, BM). MALLECO: *Puren, Bro. Claude-Joseph* 3020 (US). Nuble: *Chillán, Germain in 1855* (W, G, P, BM, GH, F), *Elwes Dec. 27, 1901* (K); *Bustamente, Bridges* 532 (syntype of *Cornidia integerrima* K, BM, G, E). OSORNO: *Philippi & Borchers Jan. 1, 1885* (BM), *Wall & Sparre* 39. TALCA: *Camarico, Moreira Feb. 1926* (GH). VALDIVIA: *Pearce* 109 (BM), *Gay* 395 (P), *Hollermeyer* 32 (UC), *Sargent in 1906* (A), *Philippi s. n.* (US, F, A), 742 (W), 651 (W), *Buchtien in 1896* (US, E, GH, BM); near Pichi, *Hohenacker* 389 (P, W, O); Los Lagos, *Behr* 1140 (MO, UC). VALPARAISO: Valparaiso, *Cuming* 398 (syntype of *Cornidia integerrima* K, BM, E). Localities uncertain or not precisely stated: *Poeppig in 1829* (type collection of *Hydrangea scandens*, isotypes MO, W), *Bro. Claude-Joseph* 2629 (US), *Shayman in 1870* (G), *Gay s. n.* (GH, P), *Hartweg* 127 (P), *Comber* 564 (E, K).

In *Hydrangea serratifolia* the inflorescence is considered to be compound, consisting of a series of cymes, one above the other, and the species is therefore placed in subsection Polysegia. However, in a few collections examined (*Bro. Claude-Joseph* 3020 and *Sargent in 1906*), the inflorescences are solitary and in one other (*Morton in 1906*), they are both solitary and compound. The pubescence on the inflorescence is also variable. Short, stiff, stellate hairs occur in some instances, while in others longer, flexuous, more dense hairs are found. Aside from these variations, however, the species is immediately distinguished from the other members of Polysegia by its short styles, resembling those of *H. Oerstedii* in the latent development of the stigmatic surface, and in its long stamens, which are three to seven times as long as the styles. Its distribution in central Chile from the province of Coquimbo to the Island of Chiloé is far to the south of that of the other species in the section Cornidia.

21. ***Hydrangea tarapotensis*** Briquet, *Annuaire Conservatoire et Jardin Botaniques de Genève*, 20: 201. 1919.

Hydrangea Bangii Engler in Engler & Prantl, *Natürlichen Pflanzenfamilien*, ed. 2. 18a: 207. 1930. Type from La Paz, Bolivia, *Bang* 1437.

Hydrangea antioquiensis Engler, *l. c.* Type from Antioquia, Colombia, *Lehmann* 4617.

Woody climbers or shrubs, branchlets and inflorescence pubescent with stellate hairs; leaves oval to obovate, broadest near middle or in upper quarter, 9-15 cm. long, 4-9 cm. wide, 1.5-2 times as long as wide; both surfaces glabrous; flowers white, all fertile; hypanthium 0.7 mm. long; calyx lobes 4, acute to broadly ovate, 0.3 mm. long; petals 4, 1.8-2.1 mm. long; stamens 8, 2-3 mm. long; styles 1 to 3, coherent in buds and more or less coherent to entirely separate during anthesis, 1-2 mm. long; mature capsules not seen. (See plate 4, figure 8.)

DISTRIBUTION: Andes of Colombia, Bolivia, and Peru from 800 to 1,500 meters elevation. (See Map 10.)

TYPE LOCALITY: Peru. San Martín: Tarapoto. Type collection: *Spruce 4349* (holotype G, isotypes C, E, GH, W, fragment and photo F).

SPECIMENS EXAMINED: COLOMBIA. ANTIOQUIA: *Lehmann 4617* (type collection of *Hydrangea antioquiensis*, isotype K). BOYACÁ: El Humbo, *Lawrence 775* (MO, G, A, E, F, K). MAGDALENA: Santa Marta Mts., *H. H. Smith, 2627* (K, US, PH, NY, F, A, S, GH). BOLIVIA. LA PAZ: Tipuani, *Bang 1437* (type collection of *Hydrangea Bangii*, isotypes F, E, PH, BM, US, GH, A, W, MO). WITHOUT PRECISE LOCALITY: *Mutis 3669* (US).

The inflorescence of *Hydrangea tarapotensis* is compound as in *H. serratifolia*, and like this species, there are occasional individuals (*Smith 2627*) in which the inflorescence is solitary. *H. tarapotensis* is distinguished from *H. serratifolia* by the coherence of its styles, which develop their stigmatic surfaces during anthesis, and its shorter stamens, as well as its somewhat broader leaves and its more northerly distribution.

22. **Hydrangea Jelskii** Szyszyłowicz, *Rozprawy Akademija Umiejetnosci wydział Matematyczno-Przyrodniczy*, series 2, 9: 215. 1895.

Woody climbers; inflorescence stellate pubescent with lax hairs, 0.3–0.5 mm. long; leaves oval, 8–13 cm. long, 3.5–7.5 cm. wide, approximately two times as long as wide; lower surface stellate pubescent, clusters of hairs borne on epidermal papillae, midrib and secondary veins prominent; upper surface glabrous or with scattered stellate hairs; petiole 0.8–1 mm. long, stellate pubescent; flowers (?) white, all fertile; hypanthium 1.5 mm. long, stellate pubescent; calyx lobes 4, broadly ovate, 0.1–0.2 mm. long; petals 4, 1.2 mm. long; stamens 8, 1–1.5 mm. long; styles 3 or 4, separate, 0.5–1 mm. long; capsule 2 mm. long, mature styles 1.5 mm. long.

DISTRIBUTION: Andes of southern Ecuador and northern Peru. (See Map 10.)

TYPE LOCALITY: Peru. Cajamarca: Tambillo. Type collection: *Jelski 332* (holotype KRA, isotypes KRA).

SPECIMENS EXAMINED: ECUADOR. EL ORO: in montaña Sichicay, near Caehicaren, tributary to Río Minas Nuevas, 2,135–2,285 m. *Steyermark 54111* (F, US).

Hydrangea Jelskii is known only from two collections and in both the specimens are mostly past the flowering stage, so that the description of the flower parts is based on only a few flowers remaining on the collection of Steyermark. From this material, the stamens appear to be shorter than those of any of the other members of this subsection, and they appear to be

no more than one and one-half times as long as the styles. This stamen character distinguishes *H. Jelskii* from *H. Mathewsii* and *H. serratifolia*, in which the stamens are considerably longer than the styles. *H. tarapotensis* and *H. Jelskii* are distinguished from each other by the coherent styles of the former. The stellate pubescence of *H. Jelskii* is not as dense as that of *H. Mathewsii* nor does it have the reddish brown color of this latter species.

23. **Hydrangea Mathewsii** Briquet, *Annuaire Conservatoire et Jardin Botaniques de Genève*, 20: 413. 1919.

Woody climbers; branchlets and inflorescence ferruginous tomentose with lax, stellate hairs 0.5–0.8 mm. long; leaves oval to oblong-oval, 10–19 cm. long, 5–10 cm. wide, 2–3 times as long as wide; lower surface rugose, the veins and veinlets prominent, densely pubescent with long, stellately branched coarse hairs borne on epidermal papillae; upper surface glabrous or with scattered stellate hairs; flowers white, all fertile; hypanthium 1–1.2 mm. long; calyx-lobes 4, acute to broadly ovate, 0.3–0.5 mm. long; petals 4, 2 mm. long; stamens 8, 3–4 mm. long; styles 2 or 3, separate, 1–1.5 mm. long, slender; mature fruit not seen.

DISTRIBUTION: Andes of northern Peru. (See map 10.)

TYPE LOCALITY: Peru. Amazonas: Chachapoyas. Type collection: *Mathews s. n.* (holotype G, photo F).

SPECIMENS EXAMINED: PERU. AMAZONAS: Chachapoyas, *Mathews 3051* (K, BM), San Carlos, *Weberbauer 7157* (F, G, GII).

Hydrangea Mathewsii was described by Briquet from a specimen with an incomplete inflorescence. Therefore, he did not realize that the inflorescence was compound and that it should be placed in the subsection Polysegia. *H. Mathewsii* is distinguished from the other species in this subsection by its ferruginous tomentum, which resembles that of *H. asterolasia* in subsection Monosegia.

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